VOLUME LXVIII NUMBER 6

THE
BOTANICAL GAZETTE

DECEMBER 1919

RELATIVE TRANSPIRATION OF CONIFEROUS AND BROAD-LEAVED TREES IN AUTUMN AND WINTER[1]

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(WITH EIGHTEEN FIGURES)

Introduction

Transpiration has been of special interest to many investigators for a long time. At first it was considered without reference to environmental factors, but later, as more observations were made and these factors were noted to have a marked effect upon the water loss, they were taken into consideration. Many of the data assembled have been limited to plants during the growing season, so that it has seemed profitable to obtain not only quantitative data on winter losses, but also a comparison of the relative transpiration of conifers and broad-leaved trees in summer and winter.

Various methods have been devised for determining transpiration, from the cut shoot potometer, which usually gives losses quite too low when compared with rooted plants (**6, 16**), to the cobalt chloride method of STAHL (**17**), recently improved by LIVINGSTON and SHREVE (**13**). With few notable exceptions, such as the method used by ILJIN (**11**), who worked on xerophytes and mesophytes in the field, the former method has been used largely for laboratory measurements, while the latter, although especially devised for field use, does not take into account the environmental

[1] Contribution from the Department of Botany, University of Nebraska, new series, no. 29.

factors of the habitat under which the plants are growing except as measured by the internal transpiring power of the plant, nor does it give a record of the continuous transpiration losses.

Unquestionably the most reliable data have been those obtained by the potometer, where the entire sealed container was weighed with the whole plant intact. A survey of the literature, however, reveals rather scant data on the transpiring power of trees, especially coniferous trees, regardless of the method employed.

That evergreen trees are constantly supplied with water, even in winter, was first observed by HALES (8), and later by DUHAMEL (4), TREVIRANUS (18), and others.

In 1860 HARTIG (10) made some investigations on transpiration losses with *Picea*, a meter high, in milder winter, and found that the plant lost from about 100–125 gm. of water a day. These figures, however, are of little value so far as calculating the intensity of transpiration is concerned, since he gave neither area nor weight of the transpiring part.

BURGERSTEIN (3) in 1875 indicated the relation of transpiration to lower temperatures, and showed that cut branches of *Taxus baccata* transpired in an hour, at $-2°$ C., 0.288 per cent, and at $-10.7°$ C., 0.019 per cent of their fresh weight.

That transpiration may take place quite rapidly at rather low temperatures has been shown by WIESNER and PACHER (22). Twigs of *Aesculus* and *Quercus*, for example, lost 0.32 and 0.25 per cent respectively of their weight in 24 hours at $-3.5°$ to $-10.5°$ C., and 0.199 and 0.192 per cent at $-5.5°$ C. to $-13.0°$ C.

BEACH and ALLEN (1) found a loss of from 4 to 9 per cent of water in apple twigs during a single week in January, with a minimum temperature of $-26.0°$ C. They found also in general that the hardiest varieties were the most resistant to water loss.

According to WARMING (20, p. 310), coniferous trees exhale much less water vapor than dicotyledonous trees, due to their xerophytic nature.

KUSANO (12) has given convincing quantitative data on the transpiration of evergreen trees indigenous to Japan. He found that evergreen trees transpired in winter an average quantity of at least 0.48 gm. per sq. dm. per day (with the exception of conifers),

or 16.58 gm. per 100 gm. of fresh weight in foliage trees, and 8.18 gm. in conifers. He also noted that the time of minimum transpiration agrees with that of the minimum temperature, which occurred at the end of January. He states further that the difference in the amount of transpiration of different species of evergreen trees becomes smallest at the time of minimum transpiration; and a change in the external conditions, especially in temperature, does not necessarily produce a corresponding change in transpiration in different species. In average cases the amount of water transpired by foliage evergreen trees is one and a half or two times greater than that transpired by conifers if we reduce the amount either to the fresh weight or to the dry weight of the transpiring part.

VON HÖHNEL (19) estimated that a birch tree, with about 200,000 leaves and standing perfectly free, would evaporate 400 liters of water on a hot dry day. He also has calculated that during the period of vegetation the beech requires 75 liters, and the pine only 7 liters for every 100 gm. of leaf substance. The same writer gives us the following table on the relative amount of water transpired from June 1 to November 30 per 100 gm. dry weight of leaf:

Birch	67.9	Oak	28.3
Lime	61.5	Red spruce	5.8
Beech	56.6	White pine	5.8
Maple	46.2	Silver fir	4.4
Elm	40.7	Austrian pine	3.2

Experiments on the transpiration of seedlings of *Acer saccharinum* in prairie and shrub thicket have been carried out by WEAVER and THIEL (21). Trees placed in the latter habitat lost only 30 per cent as much water per sq. dm. as those in the prairie. Similar experiments with *Quercus macrocarpa* gave comparable results. The high transpiration losses in the prairie help to explain the absence of trees from such localities.

BERGEN (2) compared the transpiration rates of a number of broad-leaved evergreens, including *Olea europaea*, *Quercus Ilex*, and *Pistacia Lentiscus*, with those of equal leaf surfaces of *Ulmus campestris* and *Pisum sativum*. He found that the losses in the

former group were only about 25 per cent less than in the latter, and concluded "that xerophytic leaf structure is not always incompatible with abundant transpiration, but sometimes exists only for use in emergencies to protect the plant from injurious loss of water."

HANSON (9) has shown that the major water losses from the crowns of isolated trees of *Ulmus americana*, *Acer saccharinum*, and *Fraxinus lanceolata* occur from the peripheral branches, and less than one-sixth from equal areas of leaf surface on shaded branches.

The present investigation was undertaken with a double purpose of obtaining data on the relative losses in summer and winter of conifers and broad-leaves, and also to make a beginning on the problem of winter killing of trees and shrubs. This latter project is not included in this paper.

Methods

In the spring of 1918 seedling conifers of *Pinus ponderosa* Dougl. and *Pinus Banksiana* Lamb. were obtained from the forest nursery at Halsey, Nebraska; while those of *Abies grandis* Lindl., *Pinus Murrayana* Balf., *Picea Engelmanni* (Parry) Engelm., and *Pseudotsuga mucronata* (Raf.) Sudw. were secured from the national forests of northern Idaho. These seedlings, varying from two to four years in age, were potted during May in 5-, 7-, and 8-inch pots respectively, according to the size of the plants and the demands of the root systems, and in soil consisting of two parts of rich garden loam and one part of sand, thoroughly mixed and screened through a one-fourth-inch-mesh sieve. The pots were placed on the lawn near the greenhouse until needed in late summer, and were thoroughly watered every day and sometimes twice a day during the driest periods. A few trees, mostly white fir and Engelmann spruce, died. These, with numerous weaker individuals of other species, were discarded, and only the very best plants, which showed the most flourishing condition of growth, were used in the experiments; in fact, only about half of the original stock was thus selected and used.

Galvanized iron containers with flat bottoms and straight walls were used in the transpiration work, the size varying according to

the demands of the root system. Thus, while the 2-year-old Engelmann spruce required containers only 6.5 inches deep by 3.5 inches wide (these were the smallest used), the 3-year-old yellow pines were grown during the experiments in containers 5.5 inches in diameter and 14 inches deep. Such containers are very desirable, since they combine lightness with appropriate shape for using the minimum amount of soil.

In September, when the trees were transplanted from the pots to the galvanized iron containers, they were handled in such a way as to scarcely disturb the root systems. A layer of coarse gravel 0.25 inches deep was placed in the bottom of each container, to the side of which, extending from the bottom to the top, a heavy glass tube 5 mm. in diameter was fastened with sealing wax. The soil in the flower pots, having been well watered 24 hours previous to transplanting, and the water allowed to drain through the bottom of the pot, was of such a texture that the whole contents could easily be removed by inverting the pot and jarring the edge while holding the soil surface intact with a piece of cloth. This core of soil, containing the root system practically undisturbed, was placed in the new container. In some cases it was necessary to trim away a part of the top of the conical core, but the part removed was always free from roots. Previously the sheet metal container had been filled to such a depth with soil of the same composition as that of the core, that the plant, when put in place, would be at a proper height in relation to the top of the pot. Soil samples for moisture content determinations were taken at this time. Any spaces in the new containers were carefully filled with soil which was properly compacted. Several plants had their root systems more or less disturbed in repotting, and these were discarded. Finally, the pots were sealed.

The seals consisted of petrolatum mixed with paraffin; the latter had a melting point of about 50° C. Various mixtures were used, from 80 per cent paraffin and 20 per cent petrolatum (by weight) at the beginning of the experiment, when the weather was hot, to 25 per cent paraffin and 75 per cent petrolatum in midwinter. A very satisfactory seal for winter weather consists of the latter mixture poured on the surface of the soil while very hot, and then

covered with a less plastic seal of about equal parts of the two ingredients. Little difficulty was experienced in keeping a perfect seal intact.

The broad-leaved trees, *Acer saccharinum* L., *Ulmus americana* L., and *Quercus macrocarpa* Michx., were handled in identically the same manner as the preceding, except that they were grown from seed sowed in flats in the greenhouse, but the plants were transferred to pots out of doors in June.

In order to insure uniform soil temperature conditions for all plants concerned, and changes of temperature similar to those under

FIG. 1.—Arrangement of trees in containers, with collars to insure temperature changes comparable with those of plants growing under natural conditions.

natural conditions, the containers (approximately 100 in number) were placed in tin cylindrical collars, each collar being slightly larger than its respective container. These were in rows about 6–10 inches apart and completely surrounded by soil. The top of each container and collar was covered with a heavy woolen blanket, slit to accommodate the stem, and this in turn with a piece of thick muslin waterproofed by infiltration with the hot wax seal mixture. The edges especially, and also the whole cloth, as well as the surrounding soil, were covered with a thin layer of sand. To prevent the drifting of snow among the trees thus planted on the University campus, the collars and inclosed containers were set on the bare soil surface, and the well-tamped soil filled in between them was held in place by a board frame 12 inches high (fig. 1.)

Continuous records of the humidity of the air and the temperature of both air and soil were obtained by means of Friez's hygrothermographs. The last was for a soil depth of 6 inches among the containers. A thermometer placed at a similar depth in one of the medium sized containers, and protected from external atmospheric conditions by means of a felt-lined brass case fitted with a cap, gave readings very similar to those of the soil, as may be seen in table I.

TABLE I

SOIL TEMPERATURE AT A DEPTH OF 6 INCHES INSIDE A CONTAINER, AND AT A SIMILAR DEPTH OUTSIDE IN THE SOIL

Date	Temperature among roots	Temperature outside
December 18 A.M.	1.5° C.	1.5° C.
18 P.M.	2.0	2.0
31	−4.0	−4.0
January 1	−2.5	−2.5
2	0.0	0.0
3	1.5	1.0
14	−7.5	−8.0

While the factor data will be discussed in connection with the transpiration graphs, it may be said here that at no time was the soil in the containers frozen solidly to a depth greater than 2.5–3.0 inches, a point extending not far into the root zone.

Transpiration losses were determined by weighing the containers. A large long-armed Troemner balance was used which was sensitive to 0.5 gm. under the maximum load of about 8–9 kg. imposed upon it. In making the weighings the containers were transferred from their place out of doors into a weighing room cooled to nearly a similar temperature, for, as shown by WINKLER (23), leaves of evergreens and twigs of other trees can endure from four to six times as much cold if the changes are gradual as if they are sudden. Unless the water loss was rather insignificant as compared with the amount of soil concerned, the practice followed was to replace the loss at each weighing by adding the proper amount of water from a burette through the temporarily uncorked glass tube in the side of the container. Thus the soil moisture was kept at an almost uniform condition throughout.

At least two or three times during the course of the experiments, which extended from September 1917 to May 1918, the seal was broken and the soil thoroughly aerated by means of an aspirator. An examination of containers discarded from time to time because of accidents to the aerial parts of the plants showed that at all times the soil was sweet and in good condition. Such an examination also revealed that the roots of both deciduous and coniferous trees had penetrated somewhat into the new soil. As pointed out by MACDOUGAL (14), the root growth of broad-leaves corresponds to the warm periods during which absorption is active, while any

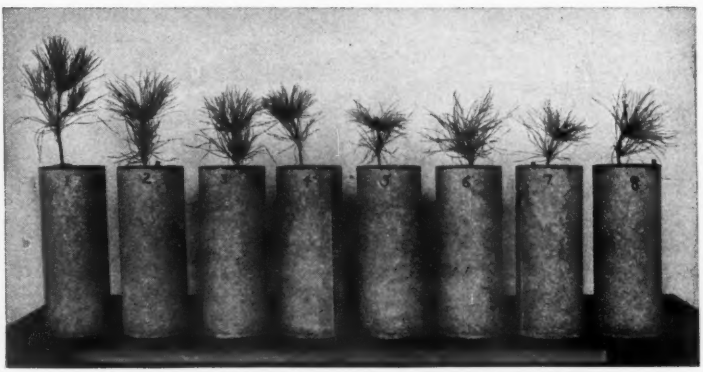

FIG. 2.—Battery of 3-year-old yellow pines; photographed February 28, 1918; none of needles fallen.

possible resting period in summer is deemed due to scarcity of water and not to any inherent tendency of the plant toward a periodicity in growth.

Pinus ponderosa

Eight 3-year-old seedlings of yellow pine were repotted, as already described, into the metal containers 5.5 inches in diameter and 14 inches deep, and the first weighings were made on September 24. This battery is shown in fig. 2. The total leaf area was determined for several of the plants the following spring and at the end of the experiment. This ranged from a minimum of 2.905 sq. dm. in plant no. 7, to a maximum of 6.428 sq. dm. in plant no. 1

(fig. 2). The areas were determined by removing the leaves from the plants, measuring the length of the leaf fascicle and the average diameter of the flat faces, as well as the diameter of the cylinder formed by the two or three leaves in the fascicle when the flat faces were appressed against each other. From these data the actual surface area was calculated. Practically no needles were shed during the winter.

Fig. 3 shows the total average daily losses of six yellow pines from September 24 to January 1. An examination of these graphs reveals a striking similarity. The highest losses are from tree

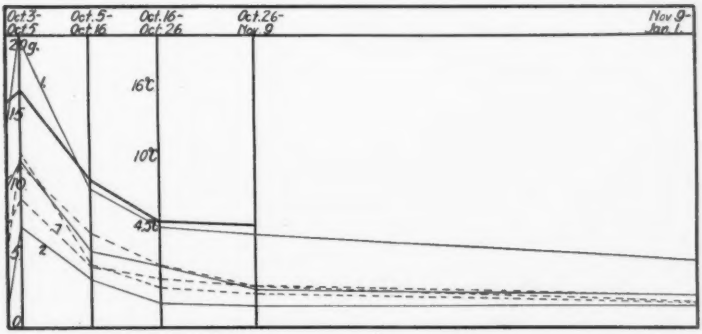

FIG. 3.—Average daily losses in grams from six 3-year-old yellow pines from September 24 to January 1; heavy line represents mean temperature for the several periods.

no. 1 with the greatest leaf area (6.428 sq. dm.), while the lowest losses are plotted from data obtained from tree no. 2, which had an area of only 4.1 sq. dm. Comparative losses per unit area are given elsewhere. Data from the other two pines were omitted in this figure for the sake of clearness. A general relation between temperature and transpiration was clearly evident. The relation to humidity was not so apparent.

The entire period from September 24 to October 16 is characterized by relatively high transpiration losses, after which there is a decided falling off. On October 11 the stomata were found to be closed. The midwinter transpiration losses are exceedingly small. Weighings made on February 7 and after a period of prolonged cold

weather (the mean monthly temperature of January being only 12.6° F.) gave total maximum losses for the entire period of 37 days of only 2.5 gm. The average total loss during this time was about 1 gm. It is surprising how an area of 3–6 sq. dm. of leaf surface can be exposed with such minimum losses. The daily losses, compared with those from the same plants during the period September 24 to October 11, are only 1/251 as great. The average losses during succeeding intervals are shown in table II.

TABLE II

TOTAL AMOUNT (IN GM.) OF WATER TRANSPIRED BY 3-YEAR-OLD YELLOW PINES FROM JANUARY 1 TO MAY 2, 1918

Plant	January 1–February 7 (37 days)	February 7–March 13 (34 days)	March 13–26 (13 days)	March 26–April 29 (34 days)	March 26–May 2 (37 days)
1	2.0	13.7	8.8	7.3	.....
2	0.5	.....	12.2	16.5	.....
3	2.5	9.5	11.0	13.5	.....
4	1.5	8.0	14.5	.....	69.0
5	1.5	7.9	16.1	.....	70.0
6	0.5	10.2	13.8	.....	26.0
7	0.5	4.5	.....	.....	.....
8	0.5	13.1	23.9	.....	91.4

A general but slow rise during the cold month of April may be noted, with a sharp increase following the milder weather in May. The transpiring area throughout is practically constant, since little growth occurred before May 1. On April 3 the stomata were found to be open.

Initial weighings from a battery of five 2-year-old yellow pines, each in a 4×9-inch container, were obtained on October 18. Two of these plants are shown in fig. 12. Table III gives the total losses during the several periods.

On December 19 the leaves were falling so badly that all but two plants were discarded, but the following spring all put out new leaves.

The exceedingly low water losses during the period December 19 to March 13 correspond with those found for the other battery of older yellow pines; in fact, this was found to be the case with all of the conifers. Table III shows an increase in the transpiring

power as spring advanced similar to that of the older pines in the other battery. These plants were growing in a soil with an average water content of 15.8 per cent (18.2 per cent maximum,

TABLE III

TOTAL TRANSPIRATION LOSSES (IN GM.) OF 2-YEAR-OLD YELLOW PINES FROM OCTOBER 18 TO MAY 2

Plant	October 18–November 17 (30 days)	November 17–December 19 (32 days)	December 19–March 13 (84 days)	March 13–April 2 (20 days)	April 2–May 2 (30 days)
1	44.0	12.0	.....	.....	.....
2	48.0	14.1	.....	.....	.....
3	42.0	4.0	.....	.....	.....
4	17.6	6.1	4.3	8.2	13.6
5	22.5	6.5	3.4	6.3	12.5

14.6 per cent minimum), and an available water content varying from 13.5 to 10 per cent.

Pinus Banksiana

A battery of eight 3-year-old jack pines in containers 4.5 inches in diameter and 10 inches deep was sealed and weighed on September 26. These trees were growing in a soil with an actual water content ranging from 8.6 to 15.1 per cent, of which only 4 and 10.3 per cent respectively were available for growth.

The leaf area, calculated in a manner similar to that already described for the yellow pines, ranged from 2.141 to 4.470 sq. dm. The plants remained in good condition throughout the winter and showed vigorous growth in the spring. In addition to the usual brownish color of the leaves in winter, however, the tips of many of the leaves died during January and February. Practically all the leaves remained on the plants throughout the experiment. Fig. 4 shows this battery as it appeared on February 28.

The transpiration losses as determined for the several periods are plotted in fig. 5. A glance at these graphs shows two things which are at once apparent. First, the general parallelism of the lines throughout (except from October 17 to 26, to be considered later); that is, the plant which gave the highest or lowest losses during the early periods continued this behavior throughout. The

actual losses are generally correlated with the leaf area; for example, the greatest losses are from plant no. 7 with an area of 4.47 sq. dm., while those in graph no. 2 are from a plant with an area of only 2.14 sq. dm. Secondly, there may be noted a rise or fall in the graphs which corresponds in general with temperature changes. After October 17 there was a gradual but marked falling off in water

FIG. 4.—Battery of 3-year-old jack pines

losses, and the rate remained very low until about the first week in April, when growth was resumed. These data are shown in table IV.

TABLE IV

TOTAL TRANSPIRATION LOSSES (IN GM.) FROM 3-YEAR-OLD JACK PINES DURING THE SEVERAL INTERVALS FROM DECEMBER 19 TO APRIL 29

Plant	December 19–February 7 (50 days)	December 19–March 26 (97 days)	March 26–April 29 (34 days)
1	.....	39.5	96.4
2	.....	14.0	36.5
3	.....	8.0	48.5
4	.....	24.5	89.9
5	.....	20.2	56.5
6	3.0	February 7–March 26 (47 days)	.....
7	2.0	12.0	.....
8	3.5	30.8	90.0

The midwinter losses, actual and relative, are just as marked as they were in the case of the yellow pines. During the period December 19 to February 7 the total average loss was only 2.8 gm., an amount which, compared on the daily basis, is only 1/169 of that lost during the autumn period (September 26 to October 17).

Abies grandis

Two batteries of white firs were used. One consisted of eight 2-year-old seedlings in containers 3.5 inches in diameter by 6.5 inches deep, and the other of eight 4-year-old trees in containers 3.5 inches in diameter and 9 inches deep.

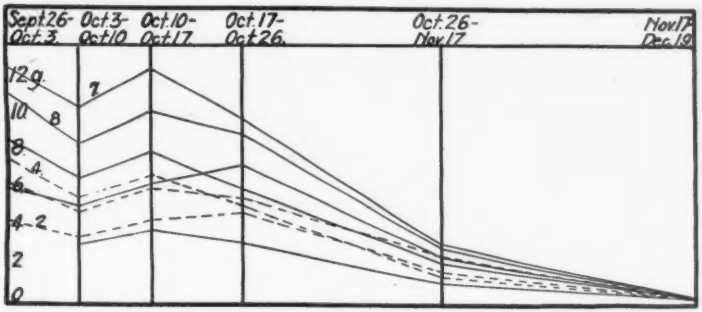

FIG. 5.—Average daily losses in grams from eight 3-year-old jack pines; September 26 to December 19, 1917.

The younger plants were growing in soil with an available water content ranging from 6 to 9.4 per cent. All were winter killed. As this did not occur until January or February, the transpiration losses up to that time are reliable. About January 15 the leaves began to drop off badly, but the leaf area of several of the plants was determined without removing the leaves, and before defoliation had begun. This was accomplished by determining the number of leaves, their lengths, and average diameters. Three of these seedlings had leaf areas of 0.0972, 0.1641, and 0.0970 sq. dm. respectively. These plants are shown in fig. 11. This picture was taken late in February after many of the leaves had fallen. Because of an accident to the top of one tree, it was discarded.

The transpiration losses from September 27 to December 12 from the seven remaining plants are shown in fig. 6. The average total loss during the period of December 12 to February 11 was only 0.7 gm., the maximum and minimum losses being 1.0 and 0.3 gm. respectively. This daily winter loss compared with that of early fall (September 27 to October 10) is only 1/55 as great. It must be noted, however, that it was during this period that the seedlings were winter killed and may have lost more water than

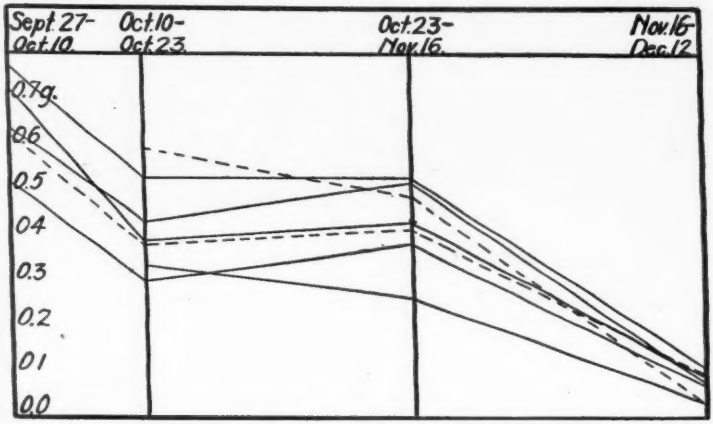

FIG. 6.—Average daily losses in grams from seven 2-year-old white firs from September 27 to December 12, 1917.

normally. On February 11 the leaves were brown and the plants appeared dead.

The 4-year-old firs, although growing under more favorable moisture conditions (from 5.3 to 13.7 per cent available moisture), also succumbed to the dry cold winter. On February 11 the leaves were all brown and dead. The transpiration losses to December 19 are reliable, however, for up to this time all the plants were in good condition. The leaves did not drop badly, even after drying, as is shown in fig. 7, a photograph which was taken on February 28. Leaf areas for plants 5 and 6 were calculated as for the other white firs. These leaf areas were 1.065 and 0.638 sq. dm. respectively.

Since weighings of both sets of firs were taken on the same days, the graphs in fig. 6 may be compared directly with those in fig. 8.

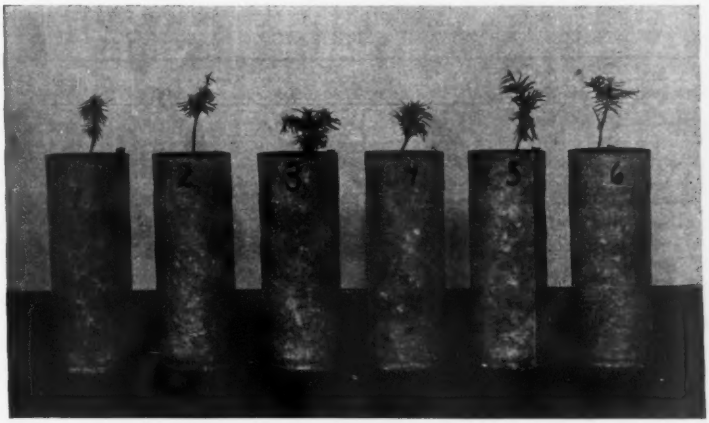

FIG. 7.—Battery of 4-year-old white firs; photographed February 28, 1918, after some of leaves had fallen.

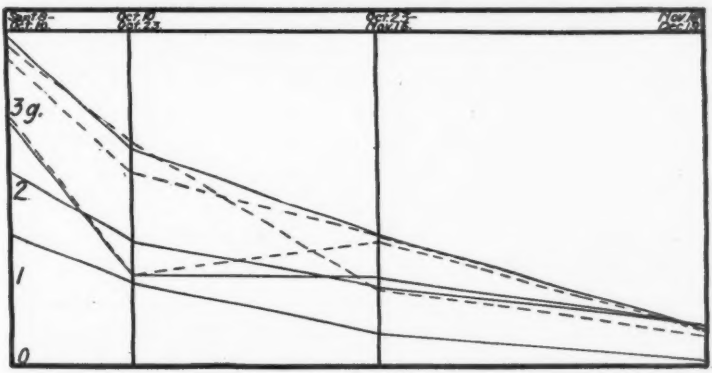

FIG. 8.—Average daily losses in grams from battery of seven 4-year-old white firs; September 28 to December 19, 1917.

A marked irregularity in the course of the otherwise generally parallel graphs may be seen during the period of October 23 to November 16.

Attention has already been called to this phenomenon in case of both the yellow and jack pines, and figs. 9 and 10 show the same occurrence for the spruce and Douglas fir. Although this phenomenon was not examined carefully at the time, for it was not known

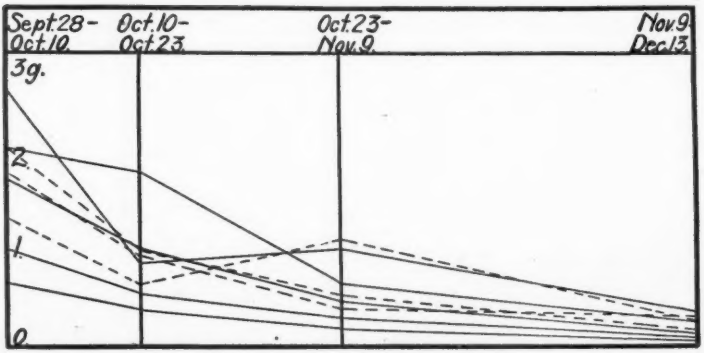

FIG. 9.—Average daily losses in grams from battery of eight 3-year-old spruces; September 28 to December 13, 1917.

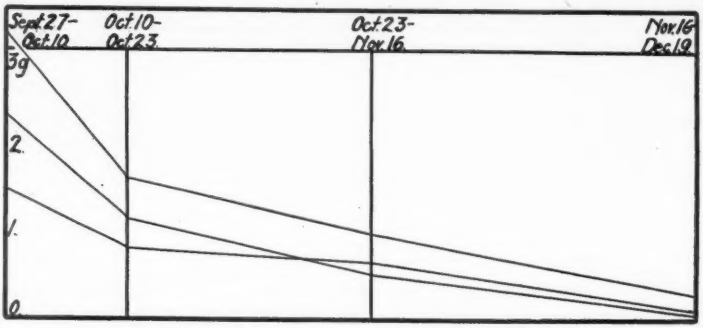

FIG. 10.—Average daily losses in grams from battery of three 3-year-old Douglas firs; September 27 to December 19, 1917.

to occur until after the final weighings on November 16 were plotted, the irregularity is probably due to the individuality shown by the several plants in the rapidity of permanent closure of the stomata, and a general slowing down of the vital activities as the temperature decreased.

Picea Engelmanni

This battery consisted of eight 3-year-old Engelmann spruce seedlings grown in containers 3.5 inches in diameter by 6.5 inches in depth, and in soil with available moisture ranging from 11.3 to 15.1 per cent.

Although the leaves dropped off badly during late December and in January, none of the plants died. All put forth a vigorous growth of new leaves during April and May of the following spring. Three of these trees, photographed in February, are shown in fig. 11.

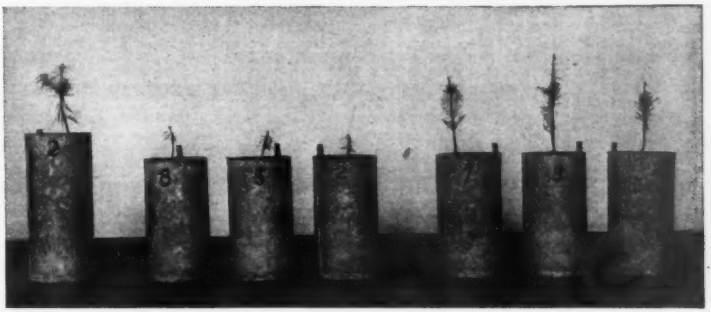

FIG. 11.—Three 3-year-old Engelmann spruces, three 2-year-old white firs, and one Douglas fir, all more or less defoliated; photograph taken February 28, 1918.

The leaf areas of three plants, calculated at the time the leaves had just begun to fall, were 2.78, 3.91, and 5.87 sq. dm. respectively. These areas were determined while the leaves were still intact by counting their total number, measuring the length and average diameter of each leaf, and then calculating the area of the four sides. The graphs giving the transpiration losses are shown in fig. 9. A comparison of the water losses from these plants with those of other conifers shows a remarkable similarity.

Pseudotsuga mucronata

Because of high mortality among the Douglas firs during the reestablishment in pots in early summer, only three 3-year-old seedlings were available for experimental work in September. These were placed in containers 3.5 inches in diameter by 8 inches

in depth, sealed and weighed on September 27. The water content of the soil in the three containers was 13.8, 15, and 18 per cent respectively. The wilting coefficient was 4.7. One of these plants is shown in fig. 11.

The leaf area of plant no. 1 was 0.3062 sq. dm. This was determined by considering the leaves as having two flat surfaces and multiplying the length of each by its average diameter.

Transpiration losses are shown from September 27 to December 19 in fig. 10. During the period December 19 to February 11, the total losses of two plants (the third having accidentally been

FIG. 12.—Battery of five 3-year-old lodge pole pines and two 2-year-old yellow pines; photographed February 28, 1918.

broken off) were 0.4 and 1.1 gm. respectively. On the basis of the average daily loss, this is a mere fraction (only 1/146) of that during the autumn period September 27 to October 10. In March the plants were discarded because of the falling leaves; in fact, one finally died, but the others showed renewed growth in the spring.

Pinus Murrayana

Still another battery of needle-leaved plants, consisting of six 3-year-old lodge pole pines, was experimented upon during the period beginning October 18. These plants, grown in containers 4 inches in diameter and 9 inches in depth, are shown in fig. 12. The water content of the soil ranged from 16.4 to 21.8 per cent.

All of the plants died in February, although the needles persisted for a long time.

The transpiration losses shown in table V are not greatly different in their amount from those of the other conifers. Likewise they show a gradual decrease as winter approaches, with minimum midwinter losses. All losses recorded are reliable because no readings were taken after the plants showed signs of deterioration.

TABLE V

TOTAL LOSSES (IN GM.) FROM A BATTERY OF SIX LODGE POLE PINES FROM OCTOBER 18 TO FEBRUARY 11

Plant	October 18–October 26 (8 days)	October 26–November 17 (22 days)	November 17–January 4 (48 days)	January 4–February 11 (38 days)
1	4.5	9.5	3.9	0.7
2	13.4	30.4	6.0	0.7
3	2.9	15.5	5.5	1.6
4	5.3	13.5	2.6	0.7
5	7.5	15.5	7.8	1.1
6	11.5	37.7	11.3	1.0

Ulmus americana

Initial weighings of a battery of 12 white elm trees were made on September 20. These plants were in containers 5.5 inches in diameter and 8.5 inches deep. A photograph taken on May 1 just when the plants were leafing out is shown in fig. 13.

The leaf areas were determined, as in the case of the other dicotyledons, by means of solio leaf prints. These were made, of course, without removing the leaves from the stems. The areas of the plants whose transpiration losses are shown in fig. 14 were as follows:

No. 6	10.28 sq. dm.	No. 10	4.15 sq. dm.
7	8.57	11	4.52
8	6.56	12	5.26
9	8.97		

For the sake of clarity, the losses from the other plants were not recorded in fig. 14. In all cases they were very similar. With the exception of plant no. 12, there is a close agreement between

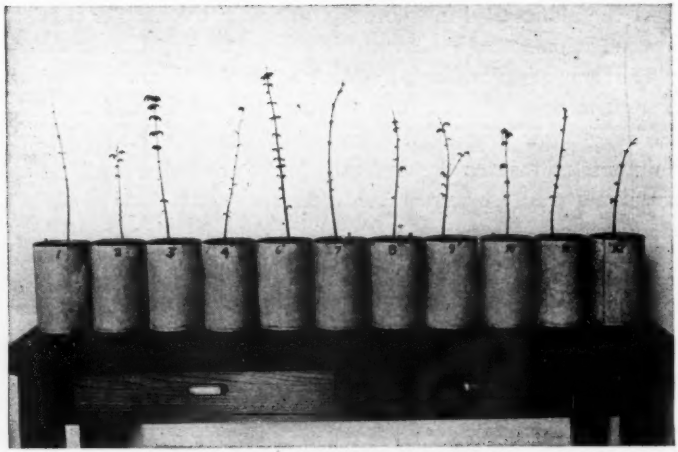

FIG. 13.—Battery of white elms putting out new leaves; photographed May 1

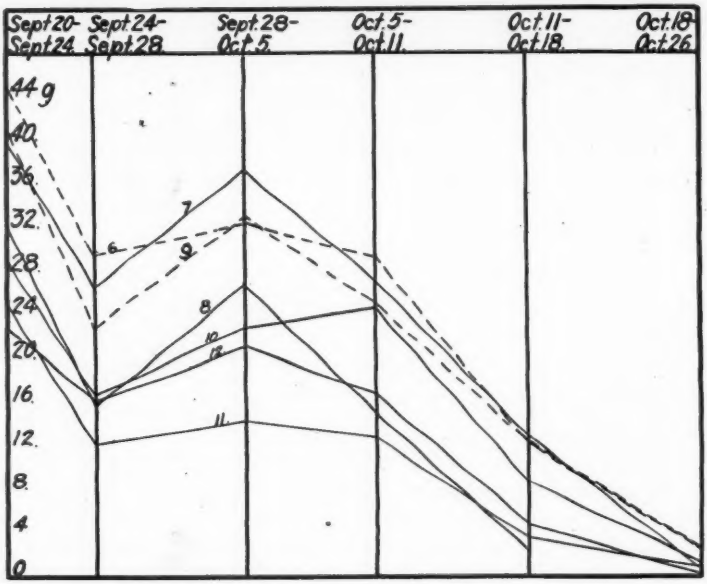

FIG. 14.—Average daily losses in grams from seven 1-year-old elm trees; September 20 to October 26, 1917.

the early autumn losses (September 20 to October 11) and the initial leaf area. Also a comparison of the graph of mean temperature for the several periods (fig. 15), with the graphs showing the march of transpiration, shows that they have a striking resemblance. The mean temperature was obtained from the thermograph records, and is given on a time-humidity basis. The means for the several periods respectively were obtained by drawing a horizontal line through the weekly record sheet in such a manner that the total area included by the graph above this line was equal to the total area below the line. The areas were determined by the aid of a planimeter. In this interpretation both temperature and time factors are taken into consideration. Temperature, indeed, seems to be the controlling factor, for no such correlation between transpiration and humidity (here the graph is inverted) is discernible after October 5; that is, transpiration dropped off at this time, following the descending temperature graph in spite of a decreasing humidity.

These two factors, however, together with wind velocity, are well summed up in evaporimeter readings. These were obtained by Livingston's porous cup atmometers and show an increase or decrease very similar to the transpiration graphs. They are as follows:

September 20–24	25.1 cc. average daily loss
September 24–28	11.8 cc.
September 28–October 6 . .	22.2 cc.

Readings were discontinued on October 11 because of freezing weather at night. Unfortunately no instrument has yet been devised for satisfactorily measuring winter evaporation losses.

The irregularity in the graphs, especially in the fourth interval, is due to the non-uniform drying out of the leaves. Up to October 5 the leaves of all the dicotyledonous plants were green and apparently functioning normally. By October 11 a few of the older basal leaves were beginning to turn brown. While some dropped at once, many held on after they were dry. This irregularity in defoliation defeated an attempt to base the daily losses upon the actual average leaf area during any given period, although an exact

record was kept of the time of the fall of each leaf, together with its area.

The transpiration graphs show a general falling off after October 11, which is not unlike that of the conifers; only here the transpiration is from a constantly decreasing area (all the leaves had fallen or remaining fragments were removed by October 26), while in the conifers the area remains constant. In table VI are given the total losses (which are too small to plot on an average daily basis) from October 26 to May 1.

TABLE VI

TOTAL LOSSES (IN GM.) FROM 12 ELM TREES FROM OCTOBER 26 TO MAY 1

Plant	October 26–November 9 (14 days)	November 23–January 4 (42 days)	January 4–April 24 (110 days)	April 24–May 1 (7 days)
1	.....	1.0	7.4	2.2
2	.....	1.0	5.6	3.2
3	6.9	1.0	12.3	12.7
4	2.8	1.0	6.6	2.7
6	3.3	1.0	11.3	9.7
7	3.4	1.5	10.8	1.3
8	2.0	1.0	5.8	3.2
9	5.7	1.5	9.3	3.7
10	1.9	0.5	7.0	5.8
11	0.4	0.5	4.5	2.3
12	1.5	0.5	7.1	2.2

From November 9 to 23 the seals were removed and the soil allowed to dry out. The loss was about 125–175 gm. They were then resealed, and 250 cc. of water was added. On April 24 some of the plants, as nos. 2, 10, and 11, had buds swollen but not yet open, while in others, as nos. 3, 6, and 7, the leaves were unfolding. On May 1 nos. 3 and 6 had leaves fairly well out, some of them being over 1.5 cm. long, while in others (as nos. 1 and 7) the leaves were just bursting from the buds.

The winter losses are very small. During a period of 42 days (November 23 to January 4) the average loss was only 1 gm. from the bare stems which exposed an area of 0.28 to 0.50 sq. dm. Table IX gives the relative transpiration losses of conifers and broad-leaved trees.

Acer saccharinum

Weighings of a battery of 12 soft maples were made on the same dates as those for the elms. The containers were of the same size,

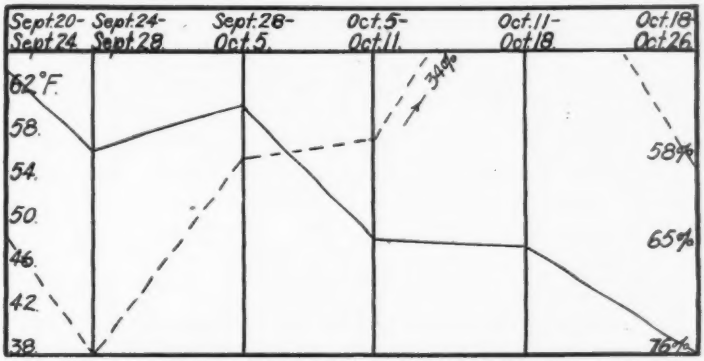

FIG. 15.—Mean temperature (solid line) and mean humidity (broken line) during several intervals from September 20 to October 26, 1917.

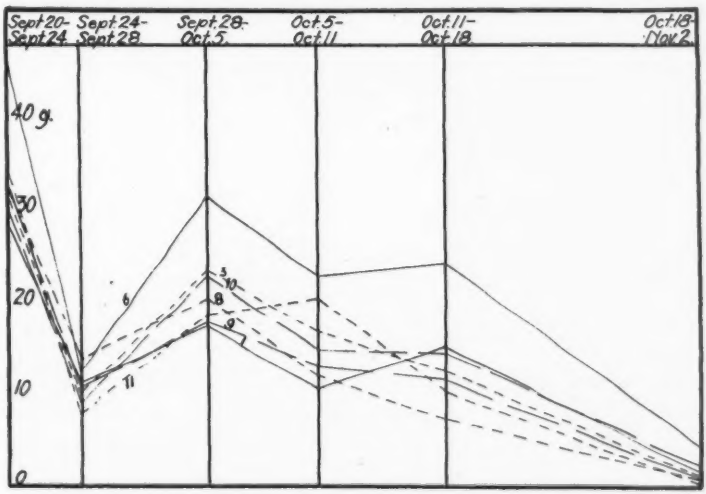

FIG. 16.—Average daily losses in grams from seven 1-year-old maple trees; September 20 to November 2, 1917.

and the batteries and the methods of handling them were so similar throughout that further description will be unnecessary.

The leaf areas ranged from 11.32 sq. dm. in plant no. 6, which gave the highest losses throughout (fig. 16), to 6.47 sq. dm. in no. 11, where the transpiration losses are among the lowest. A good correlation existed between leaf area and the magnitude of the losses. To avoid confusing a multiplicity of lines, data from five of the maples have been omitted in this figure. The data of these five trees are very similar to those shown.

TABLE VII

TOTAL LOSSES (IN GM.) FROM 12 MAPLE TREES FROM NOVEMBER 2 TO MAY 1

Plant	November 2–16* (12 days)	November 28–January 1 (34 days)	January 1–April 24 (113 days)	April 24–May 1 (7 days)	Condition on on May 1
2.....	2.2	0.8	2.9	3.6	Two buds unfolding leaves
6.....	2.5	0.8	4.5	2.2	Just showing signs of life
8.....	3.0	1.1	.....	.....	.....
10.....	1.7	0.3	3.6	70.1	Leaves 1–5 cm. long
12.....	1.8	0.5	2.3	13.5	Two buds with leaves 2 cm. long
	December 6–January 1 (26 days)				
1.....	1.8	.....	.....	.....	.....
3.....	2.0	.....	3.7	4.0	One bud swollen; two others partly open but frozen
	November 2–16* (14 days)				
5.....	1.5	0.9	.....	.....	.....
7.....	2.0	1.8	.....	.....	.....
9.....	1.5	1.0	.....	.....	.....
11.....	2.5	0.5	.....	.....	.....

* All leaves off.

As in the case of the elms, a close correlation exists between transpiration, evaporation, and temperature (fig. 15); in fact, the general trend of the graphs is strikingly similar to those of the elms. The same irregularity is shown during the period of defoliation. On October 26 only the bare stems remained; these had a surface area of 0.22–0.48 sq. dm.

Further losses from November 2 to May 1 are given in table VII. The small losses are again evident, followed by a rapid rise

accompanying the unfolding of the buds. Six plants were winter killed, and no losses were recorded for them after January 1.

Quercus macrocarpa

A number of bur oak seedlings were grown from acorns obtained from an Illinois nursery in May 1917. Seven of the lot were finally selected for experimental work. These were repotted in containers 5 inches in diameter and 7 inches deep. They may be seen in the foreground in fig. 1. The initial available water content of the soil ranged from 11.3 to 15.2 per cent, but the soil moisture was reduced by evaporation from the surface of the several containers

TABLE VIII

AVERAGE DAILY LOSSES (IN GM.) OF BUR OAK SEEDLINGS FROM SEPTEMBER 24 TO JANUARY 4

Plant	September 24–October 3 (9 days)	October 3–10 (7 days)	October 10–18 (8 days)	November 1–16* (15 days)	December 7–January 4 (28 days)
1.....	9.0	7.0	2.1	0.25	1.0
2.....	.....	11.0	4.9	0.55	1.3
3.....	10.2	6.4	4.3	1.22	1.4
4.....	15.5	9.9	1.1	0.26	1.8
5.....	7.2	3.4	0.4	0.21	1.0
6.....	4.5	2.6	0.5	0.28	1.0
7.....	15.2	12.9	8.0	1.89	1.8

* At this time all the leaves had fallen, and the losses are not calculated on the average daily basis, but on the total loss for the entire period.

to a minimum of 4.4 and a maximum of 9.6 per cent respectively from October 18 to November 1. After this the seals were again replaced and half of the containers brought back to the original water content. The transpiration losses are shown in table VIII.

The gradual falling off in the transpiration rate without any increase, as in the case of the elms and maples, may be explained by an examination of the dates, which show that the first loss was not recorded until a time (October 3) when all the trees show a steady decrease. By November 1 all of the leaves had fallen (or the dried leaves were removed). Following this the losses are extremely small. The stem areas of the oaks were only 0.039–0.088 sq. dm.

Relative transpiration rates

Thus far we have considered largely transpiration losses of different individuals of the batteries of the various species, with only occasional reference to comparative losses of different species. It may be well, therefore, to present data showing the actual losses of different species based upon unit area. These data have been summarized in table IX. While the dates between readings are not synchronous in all cases, they are at least nearly so, and fig. 15,

TABLE IX

COMPARATIVE TRANSPIRATION LOSSES FROM UNIT AREAS OF SURFACE OF BROAD-LEAVED AND EVERGREEN TREES

Species	No. of trees	Time	Average loss per sq. dm. per day
Acer saccharinum	9	September 24–October 5	2.66
Ulmus americana	9	" 24– " 5	3.56
Quercus macrocarpa	7	" 24– " 3	5.18
Picea Engelmanni	3	" 28– " 10	4.18
Abies grandis (2 years old)	3	" 27– " 10	5.44
Abies grandis (3 years old)	2	" 28– " 11	4.76
Pinus ponderosa	3	" 24– " 5	4.20
Pinus Banksiana	3	" 26– " 10	4.80

which gives the temperature and humidity, together with the record from the atmometers, shows that the overlapping periods are quite uniform.

Relative midsummer transpiration rates of broad-leaved trees and conifers

During the following summer, while the writers were carrying on other investigations in the Rocky Mountains of the Pike's Peak region of Colorado, opportunity was afforded to compare the summer transpiration rates of different tree species.

Seedlings of white elm and soft maple grown from seed at the Alpine Laboratory near Manitou, Colorado, and at an altitude of 8000 ft., together with mountain maple (*Acer glabrum* Torr.) obtained from the forest, were the broad-leaved species used. Yellow pine, Douglas fir, and Engelmann spruce were the conifers employed. The pines were secured from the Fremont Experiment Station; while the other trees, like the mountain maples, were

transplanted into appropriate sized containers directly from the forest floor, without disturbing the root system. Care was taken

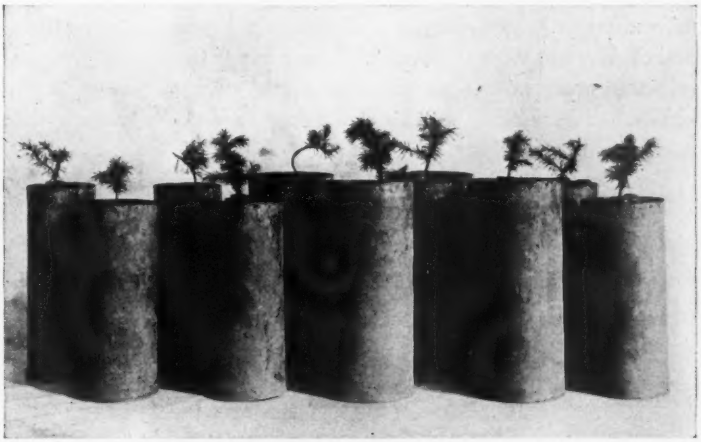

FIG. 17.—Battery of Douglas firs and Engelmann spruces from which summer transpiration losses were obtained.

FIG. 18.—Battery of yellow pines and mountain maples used for determining relative summer transpiration.

not to select these species from too dense shade. Some of these trees are shown in figs. 17 and 18.

The extra soil necessary to fill these containers was in all cases a mixture of two parts of garden loam and one part of fine gravel. It had a wilting coefficient of 10.7 per cent, and was kept rather uniformly at a water content of about 20 per cent. The methods used throughout were the same as those already described. Original weighings were not taken until after the trees had been in the containers two weeks. At this time rabbits attacked the deciduous trees and injured all but five of them.

On July 20 the remaining trees in their containers, 19 in number, were weighed to the nearest half gram. As during the preceding interval, they were then placed in a row in the soil and in such a position that all were shaded for a few hours in the afternoon.

TABLE X

AVERAGE TRANSPIRATION LOSSES PER UNIT AREA FROM SEVERAL SPECIES OF TREE SEEDLINGS

Species	No. of plants	Average loss per sq. dm.
Pinus ponderosa	4	58.2
Pseudotsuga mucronata	5	50.7
Picea Engelmanni	5	58.3
Acer glabrum	4	112.5
Acer saccharinum	1	139.3

At the end of 26 days, on August 15, they were again weighed, the leaf areas determined, and the losses calculated as in the preceding experiments. These data are shown in table X.

These data show that the losses from the various species of conifers, growing in the open but under conditions where all were shaded for a portion of the day, are very similar, and only about half as great as those of the broad-leaved species. The midsummer average daily loss per square decimeter from the yellow pines and Engelmann spruce at the Alpine Laboratory, when compared with that of the same species during the autumn at Lincoln, was found to be only about half as great at the former station. Because of the limited number of plants used, however, these data should be considered indicative rather than conclusive.

Conclusions

A consideration of the foregoing data leads us to some conclusions quite the converse of statements generally current in ecological-physiological literature. Perhaps the most important of these are the facts shown to hold under the conditions of these experiments; first, that broad-leaved trees under late summer conditions have no greater and indeed often a smaller transpiring power, area for area, than conifers; and secondly, that the water losses of coniferous trees during the winter months are relatively no greater with the needles intact than are the losses from deciduous trees after the leaves have fallen.

The fact that all of the plants concerned, including three species and about 30 individuals of broad-leaved trees, and six species represented by about 70 individuals of conifers, gave results which without exception point to these conclusions, leaves little doubt as to the validity of the finds. These results were obtained with all the plants under uniform conditions of soil type and texture, soil temperature, and identical aerial environment. The only variable factor was soil moisture, and here the range was no greater for the one group than for the other. Although the experiments were undertaken near the end of the summer, for a period of a few weeks, after their beginning the deciduous trees were in excellent growing condition, and the comparative losses as here recorded occurred during the earlier part of this period, when the weather was similar to that of midsummer as regards temperature and humidity.

That winter losses from the same leaves that transpired so freely the preceding fall and again in the following spring are so small is certainly testimony of the ecological efficiency of coniferous leaf structure for reducing water losses. Whether this is due entirely to stomatal closure, or, as seems more probable, is connected with chemical changes in cell contents as well, remains to be determined. Such work as that of MIYAKE (15) on the food making of coniferous leaves in winter and EHLERS (5) on temperature is rapidly throwing considerable light upon the winter activities of coniferous trees.

The gradual decline of the transpiring power of broad-leaved trees preceding defoliation and during the formation of the abscisslayer is what might be expected, but is heretofore, we believe, unrecorded. Weather conditions play an important part in hastening or retarding this process, and as a result the dropping off in the transpiration graph. These graphs are surprisingly similar in their general trend to those of conifers where the leaves are intact.

The spring of 1918 was unfavorable for rapid leafing out or renewed growth of trees. Consequently the increased transpiring power, which is in a direct ratio with the leaf area, occurred very gradually, and here again was not greatly unlike that of the needle-leaved trees. Undoubtedly under very favorable weather conditions, as occur during some springs, the transpiring power might easily double or treble day by day for a rather long consecutive period.

Summary

1. Autumn transpiration losses from conifers are just as great as or even greater than those from broad-leaves.

2. The decrease in water losses from broad-leaved trees resulting from defoliation is gradual, and not greatly unlike the decrease shown in the transpiring power of conifers.

3. Winter transpiration losses from conifers are only 1/55–1/251 as great as those in autumn.

4. The increased losses of broad-leaved trees in spring occasioned by foliation are in proportion to the leaf areas exposed, and are closely controlled by weather conditions, but in the main are similar to increased losses of conifers.

5. Winter transpiration losses from conifers are scarcely greater than those from defoliated stems of broad-leaved trees.

The writers are indebted to Dr. R. J. POOL for his kindly interest and encouragement, and to Dr. L. J. BRIGGS for wilting coefficient determinations; also to Mr. J. HIGGINS, of Halsey, Nebraska, and Mr. T. J. LARSEN, Priest River, Idaho, for tree

seedlings from the nurseries, and to Professor T. J. FITZPATRICK for careful reading of the manuscript and proof.

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TORSION STUDIES IN TWINING PLANTS

H. V. HENDRICKS

(WITH SIX FIGURES)

Introduction

This paper deals with a certain phase of the physiology of twining plants. It is an account of some experiments upon the scarlet runner or flowering bean (*Phaseolus multiflorus*) and the black or corn bindweed (*Tiniaria Convolvulus* [L.] Webb and Moq.), in which a modified form of auxanometer was used. To a limited extent the hop (*Humulus Lupulus* L.) was studied also.

The attention which twining plants have received from many observers has resulted in considerable literature on the subject. The main facts, however, have been well summarized by VINES[1] and by PFEFFER.[2] A résumé of these accounts seems unnecessary for our present purpose, but it is convenient, as well as in accord with the views of these workers, to consider the phenomenon as involving the following as its most striking factors: (1) circumnutation of the growing tip; (2) winding of the stem about its support; (3) torsion of the stem in the same direction as the winding (homodromous); (4) torsion in the opposite direction (antidromous). The relation of these factors to one another is not perfectly understood, and I shall not enter into any discussion regarding it. This paper deals only with torsion of the stem.

Not having ready access to the literature, the aid of Mr. PETER J. KLAPHAAK, of the University of Michigan, was secured in looking up references, and I desire to express my appreciation of his services. In as extensive a review as it was possible to make, no reference was found to any method of approaching the problem similar to the one here described.

[1] VINES, S. H., Lectures on physiology of plants. 1886.

[2] PFEFFER, W., Physiology of plants, translated by A. J. EWART, Vol. III. 1906.

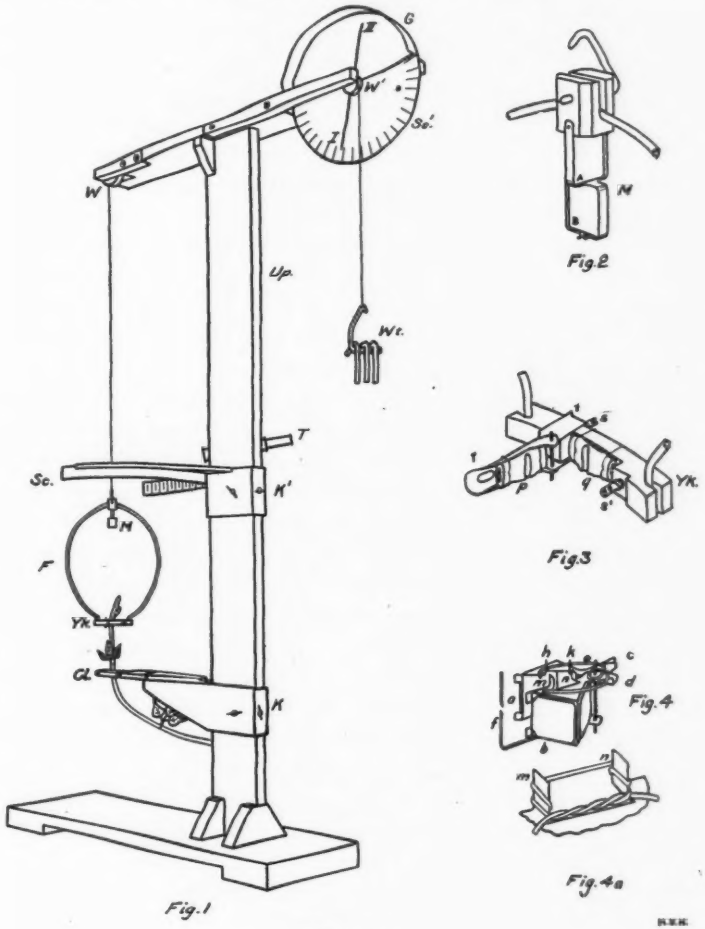
Method

The method consisted in stretching vertically a growing internode, or parts of two adjacent internodes, and measuring the amount of twist and the corresponding length. The object of this stretching is, while giving support, to eliminate twining proper, and the amount of stretching is slightly greater than that required to accomplish this. An estimate of the torsional rigidity at different lengths was also made. In certain experiments I have compared this with the diameter and with the amount of lignification. I have also begun studies on antidromous torsion, and have made a few other observations.

The apparatus is illustrated in figs. 1–4. There stands on a base an upright (*Up*) about 1 m. high. This has a top piece bearing two wheels (*W* and *W'*), over which runs a fine silk thread. On the upright are also two sliding clamps (*K* and *K'*), which can be secured at any height. The lower of these (*K*) has an arm bearing a special kind of clamp (*Cl*) for holding the lower part of the growing internode. The other (*K'*) carries a telescope (*T*) and a semicircular scale (*Sc*), which is graduated on the inside so as to read half-degrees. I found 28 cm. a convenient diameter for this scale. The upper part of the internode used is held by the frame (*F*), which is suspended by the silk thread already mentioned. The weight (*Wt*) supplies the proper amount of tension. By means of the scale (*Sc'*), graduated so as to read 0.1 mm., and the double pointer (*I*, *II*) on the wheel (*W'*) the increase in length can be obtained accurately, while this value can be obtained roughly by means of a linear scale hung near the thread on this side of the apparatus, but omitted from the figure for the sake of clearness. There is a curved guard (*G*) to protect the pointers.

The frame (*F*) requires more detailed description. It consists of a bow of heavy wire, 2.2 mm. thick and about 12 cm. in diameter, closed by a yoke (*Yk*) and suspended by a block of wood which holds four mirrors (*M*). These mirrors (fig. 2), each one 1.2 cm. in diameter (or better 1.0 cm.), are arranged in two pairs at right angles, and are held together by means of a piece of sheet metal (best of aluminum), which is cut to resemble roughly a cross and then bent into the form shown. These mirrors are held in place

by fine wires and are labeled *A*, *B*, *C*, *D*. The yoke (*Yk*, fig. 3) is a curved piece of hard wood (about 5×1×0.6 cm.) and has fitted



FIGS. 1–4

over it a piece of "tin" (*t*), which is approximately U-shaped, with the "base" of the U back of the yoke. Its position on the yoke can be regulated by means of a peg on the small screw (*s*), only a

little of which can be seen in fig. 3. This peg is between the yoke and the base of the U-piece. Another piece of "tin" (*r*) is hinged upon *t* by a pin, and has fastened to it by fine wire a rubber pad (*p*). Another rubber pad (*q*) is fastened to the yoke. These pads are pieces of 4 mm. rubber tubing (even smaller can be used for some purposes), and each has a groove cut a little more than halfway around it before it is secured in place. A slot in *r* fits over the screw (*s'*) when *r* is closed, and then the grooves on the two pads come together and make a place for holding the stem. A peg through the screw (*s'*) keeps this clamp closed. By adjusting the screws (*s* and *s'*) the correct amount of pressure required to hold the stem from slipping without interfering with its growth is obtained. This is easily determined by a few trials. The entire frame weighs about 20 gm. The clamp for holding the lower part of the stem used is constructed in the same way.

In order to keep tally on the number of complete revolutions which the stem makes in twisting, a black thread (the fine silk thread being white) is attached to the upper part of the bow of the frame, and, allowing plenty of slack, is then carried over a hook near the wheel (*W*). The number of times this is coiled (very loosely) about the silk gives the amount of twist roughly, while it is given exactly by means of the mirrors, telescope, and semicircular scale. For the sake of clearness this black thread also has been omitted from the figure.

One other device which, although imperfect, was found useful in studying intermediate points in the part of the stem used is here described and is illustrated in figs. 4 and 4*a*. I call it a "mirror clamp." It consists of two symmetrical halves (*a* and *b*) cut out of aluminum and bent into shape as shown. These halves are hinged together at one edge, and when closed form essentially a cube without a bottom. A mirror of quite thin glass, about 1 cm. square, is held in place on each side of the cube with bits of adhesive plaster. The clamp is opened by means of holders (*c* and *d*) on the two halves, and it is kept closed by means of the steel spring (*e*). On the top of each half there are two projections (*h*, *k* and *m*, *n*). Fig. 4*a* shows with enlargement how a piece of stout thread is placed on one pair of these. It is not tied, but the ends are twisted

about each other several times (more than shown). On h, k two loops of this thread are placed, instead of one, and in such a way that the inner part on m, n comes between the inner parts of the two loops on h, k when the clamp is closed. A piece of fine copper wire (f), several cm. long, is attached to one-half of the clamp. This can be adjusted by bending so as to counterbalance the holders opposite. The entire device weighs somewhat over 1 gm. Since the mirrors are placed at some distance from the vertical axis, slight corrections are necessary for accurate work. In order to measure the growth in length of the point holding this clamp, a linear scale, fastened vertically, was used. With care this measurement could be made with fair accuracy.

In its simplest terms, torsional rigidity may be looked upon as "resistance to twisting." In earlier experiments it was estimated by balancing a measured deflection in the part of the vine used against a measured twist in a very fine wire. As this required additional apparatus, as the readings were rather difficult to make satisfactorily, and as the results were not very accurate, it will not be described in detail. The success of the present method, which is not open to these objections, depends on making the frame light, compact, and with small resistance to the air. In making a determination by the present method, the period of oscillation of the frame is timed. This is, in fact, a common method in physical laboratories. As may be learned from any textbook in physics,[3] the law governing this may be stated as follows: If a circular wire of length L and radius of cross-section R suspends a body whose moment of inertia is K, and if the coefficient of torsional rigidity of the material of this wire is n, then the period of oscillation in seconds of this body is given by the following equation: $T=(1/R^2)\sqrt{8\pi KL \div n}$. From this, $n=8\pi KL \div T^2R^4$. It is more convenient, however, to use the diameter (D) of the vine, and I always use the same frame and am dealing with comparative values only. Consequently, the expression actually used is $L \div T^2D^4$, which equals what may be called *the coefficient of rigidity*. This may be defined for our purposes as *the relative measure of the resistance offered to twisting through a unit angle of an average unit length*

[3] For example, WATSON, W., A text-book of physics. Longmans, Green & Co. 1900. p. 205.

of vine per average unit diameter. As in most of the experiments no accurate measurements of the diameter were made, the expression more commonly used is $L \div T^2$. I shall call this simply *the rigidity,* or *the relative resistance to twisting through a unit angle of an average unit length of the vine.* Certain objections to these terms will be discussed later. As will be seen, they are not constant, but vary.

These experiments were performed in a greenhouse and have extended over several seasons. Generally speaking, conditions were found satisfactory for growth only during May, June, and the first part of July, at least in this particular greenhouse.

The apparatus is set up on a bench and leveled so that the upright is plumb. A weight placed on the base and wires from near the top of the standard to the roof of the greenhouse give the apparatus stability. By means of slots and screws in the top piece and in the arm of the clamp (*K*), adjustments are made so that the vertical line to be taken by the silk and the part of the vine used passes through the center of the semicircular scale. The proper weight is then applied to the silk, and the upper part of the growing internode near the tip is clamped in the frame. The lower part of this internode, or the upper part of the next internode, is then very carefully secured by the clamp (*Cl*).

Measurements of diameter were made by means of a gauge similar to one form of wire gauge. This consists of a pair of straight-edges, one of them graduated, held securely together so as to make a V with a very small angle. Usually many readings were taken (about 10–40), but irregularities in the stem prevented much accuracy. It was not found possible to make many such measurements in the case of the black bindweed. General observations of weather and temperature were recorded, but were found to be of only limited value.

Data and curves

Table I contains in an abridged form the data of a typical experiment. The dates and times of the readings are given with the corresponding lengths and the corresponding amounts of total twist in angular degrees. The average periods of oscillation of the

frame are given. This value, in seconds, is obtained in each case by observing the length of time required for a certain number of oscillations (usually 50 or 100, occasionally 200), making usually 4 or 5 determinations in each case. The average diameters are given. In some cases these were not measured directly, but were obtained from the diameter curve. The calculated values of rigidity ($L \div T^2$) and of coefficient of rigidity ($L \div T^2D^4$) are also given.

TABLE I

FLOWERING BEAN

No.	Date	Time	Length = L in gm.	Twist in degrees	Period of oscillation in seconds = T	Diameter in mm. = D	D^4	Rigidity = $L \div T^2$	Coefficient of rigidity = $L \div T^2D^4$
1.....	6–4–18	1:15 P.M.	2.00	0	2.22	1.50	5.06	0.41	0.080
2.....	6–5–18	7:55 A.M.	3.22	62	2.06	1.56	5.93	0.76	0.128
3.....	6–5–18	7:22 P.M.	5.18	391	2.32	1.67*	7.78	0.96	0.124
4.....	6–6–18	11:25 A.M.	7.24	713	2.05	1.80	10.50	1.72	0.164
5.....	6–6–18	6:05 P.M.	8.35	894	1.91	1.85*	11.70	2.29	0.196
6.....	6–7–18	9:25 A.M.	9.58	1078	1.70	1.91*	13.30	3.32	0.250
7.....	6–7–18	8:00 P.M.	10.01	1128	1.00	1.90	13.01	10.01	0.770
8.....	6–8–18	2:57 P.M.	9.92	1108	0.75	.....	.....	17.60	.....
9.....	6–8–18	5:55 P.M.	10.00	1105	0.72	1.92	13.60	19.30	1.419
10.....	6–9–18	7:20 P.M.	10.08	1102	0.65	1.96	14.75	23.86	1.617

* Value obtained from diameter curve: points *a*, *b*, and *c*, fig. 5.

In fig. 5 these data are presented in curves. In all cases abscissae represent lengths. It will be observed that in the twist curve there is relatively little slope at first, but that this slope increases later; and that at the end of the curve there is a slight but sudden and distinct drop. In other words, at first the internode twists only a little as it grows; later it twists faster; and, when the full length has been attained, there is a slight reverse twist. Note in table I that reading no. 8 shows a slight decrease in length. This was frequently observed at or near the end of growth in other experiments. It is probably due, for the most part at least, to a temporary shortening of the silk thread on account of changes in humidity. It may mean also a slight coiling of the internode. As it probably does not mean an actual shortening, this reading is not plotted in the curve. Reading no. 9 is also omitted from the twist curve.

The rigidity curve shows at first only a slight upward slope, but when the internode is approaching its full length there is a sudden and extensive upward turn in the curve. The coefficient of rigidity

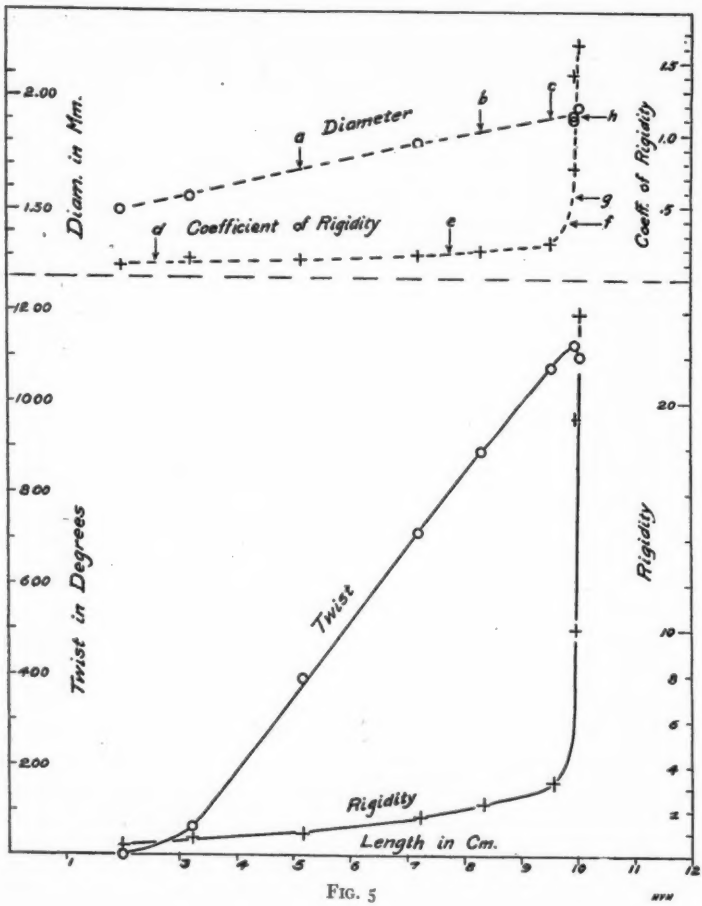


FIG. 5

curve shows the same general properties, but careful study shows that its first slope, that is, up to the point *e*, compared with the initial value of this coefficient, is much less than the ratio between

the corresponding values in the rigidity curve. This demonstrates that increase in diameter accounts to a great extent for increase in rigidity during most of the internode's growth, but does not at all account for the final increase in rigidity.

Many experiments were performed under somewhat different conditions. The results of a few of these are presented graphically

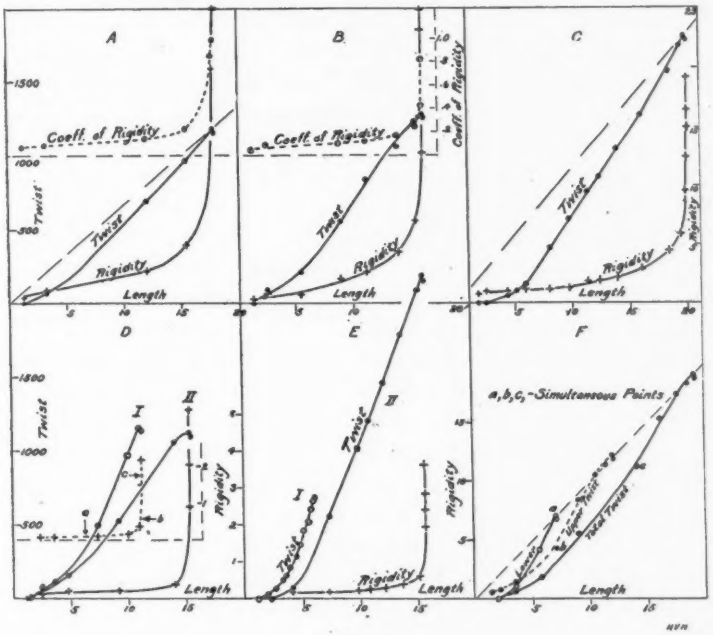


FIG. 6

on a smaller scale in fig. 6, while some of the important data are given for purposes of comparison in table II. The curves of twist, rigidity, and coefficient of rigidity show the same characteristics as those already outlined for fig. 5. It should be mentioned, however, that the final drops in the twist curves in fig. 6 have necessarily been more or less exaggerated. Curves *D*–I and *D*–II are for black bindweed, where the torsion is in the opposite direction from that in the flowering bean, being in the same sense as the thread

of a right-handed screw in the latter, while it is in the same sense as that of a left-handed screw in the former. The rigidity curves for the bindweed are much smaller in dimensions than for the bean. It will also be noticed that differences in diameters account to a great extent for differences in rigidity curves in general.

Curve *E*–I is interesting in that it shows that when the healthy vine is limited in its growth by unfavorable conditions the same rules as to twisting apply. Even in this case there was, as a matter of fact, a slight reverse twist at the end, although the figure does not show it. On the other hand, under distinctly adverse conditions (as when the greenhouse became too hot and too dry), not only was the growth itself stunted, but the torsion was quite irregular. The resulting plant in such a case could hardly be regarded as healthy.

Curves *E*–II are also interesting. Here at the beginning of the experiment the growing tip was purposely removed, but not the leaf at the upper node, which was just above the clamp in the frame. This produced no apparent effect upon the two curves. On the other hand, in some experiments the vine just below the upper node was pinched accidentally, after which that internode died. In this experiment, however, it was observed that the stump above the upper node grew 2 or 3 cm. during the experiment and exhibited apparently a normal amount of twist. In the meantime a new bud appeared at this node.

One more interesting point is shown by curves *F*. Two adjacent internodes were fastened in the apparatus and were measured for length and twist in the usual way, while the behavior of the node between them was studied by means of the mirror clamp (fig. 4). From the resulting data three curves were obtained: one for the part below the node, one for the part above, and one for the total. These curves are plotted together and then a straight line is drawn from the "zero" point to the top of the total curve. The tops of the other two curves fall approximately on this line also. This shows that in a limited portion of the vine, where torsion is taking place freely, the final amount of torsion per unit length is uniformly distributed. If a single internode had been studied in this way, presumably a similar result would have been obtained. This

TABLE II

No.	Date of experiment	Species	Internode	Diam. at end of exp. in min.	Tension net wt. in gm.	Weather conditions	Curves	Remarks
1.....	June 4 to 9, 1918	Flowering bean	7th on branch from first node	1.96	10	Largely cloud	Fig. 5	.....
2*.....	May 31 to June 3, 1918	"	13th	2.25	10	Largely sun	*A* in fig. 6	Final twist = 66° per cm.
3.....	May 26 to 31, 1918	"	11th	2.36	10	Largely cloud	*B* in fig. 6	Final twist = 79° per cm.
4.....	May 10 to 20, 1918	"	5th and 6th	2.1	10	Mostly sun	*C* in fig. 6	Final twist = 90° per cm.
5.....	June 29 to July 4, 1918	Black bindweed	12th	1.0	5	Rain and sun	*D*–I in fig. 6	Twist opposite from bean
6.....	June 26 to 29, 1918	"	17th and 18th	1.3	5	Mostly sun	*D*–II in fig. 6	Twist opposite from bean
7.....	Sept. 21 to 30, 1915	Flowering bean	8th and 9th	About 1.0	13	Sun, rain, cloud	*E*–I in fig. 6	Growth under unfavorable conditions
8.....	June 9 to 17, 1918	"	.....	1.5	10	Mostly sun	*E*–II in fig. 6	Tip removed
9.....	June 12 to 18, 1918	"	11th and 12th on branch at first node	2.1	10	Sun and cloud	*F* in fig. 6	Study of twist in 2 parts

* Nos. 2, 3, and 4 from same plant.

conclusion, however, does not hold for the vine as a whole. This is illustrated by the straight slope lines with curves *A* and *C*, fig. 6, which were obtained from widely separated parts of the same vine. Compare also the final twists per centimeter for nos. 2 and 4 in table II.

Lignification studies

The fact that increase in diameter does not account for the final development of rigidity has already been mentioned. It occurred

TABLE III

LIGNIFICATION TESTS; FLOWERING BEAN

No.	Internode	Length in cm. = L	Period in sec. = T	Diam. in mm. = D	$\frac{L}{T^2D^4}$	Amount of tissue stained with phloroglucin and HCl	Corresponding points on the coefficient of rigidity curve; fig. 5
1..	n*	1.3	1.92	1.5	.07	Only small vessels in vascular bundles	.....
2..	n−1, upper half	1.9	0.93	2.2	.09	Same as in 1, only vessels larger	*d*
3..	n−1, lower half	1.9	0.53	2.5	.17	Vessels larger than in 2; narrow ring of xylem slightly stained	*e*
4..	n−2, middle of upper half	1.8	0.40	2.3	.40	A definite ring of well-stained xylem	*f*
5..	n−2, middle of lower half	1.8	0.40	2.1	.58	Xylem more heavily stained, that is, thicker walled elements	*g*
6..	n−3, upper half	4.0	0.47	2.0	1.14	Xylem still more heavily stained; more contrast between 6 and 4 than between 5 and 4	*h*

* The terminal part; the number of this internode was not counted and so is called *n*.

to the writer that studies in lignification might be useful. For this purpose rigidity and its coefficient were determined on adjacent parts of stems of the flowering bean and of the black bindweed, and free-hand sections from the middle of each specimen were treated with 5 per cent phloroglucin followed by strong HCl.[4] In this way the lignin was stained reddish violet. In tables III and IV the data are given for two such experiments. When the observa-

[4] CHAMBERLAIN, C. J., Methods in plant histology. University of Chicago Press. 1905. p. 62.

tions in table III are correlated with the points *d*, *e*, *f*, *g*, and *h* on the coefficient of rigidity curve in fig. 5, it is seen that the growing internode does not show much rigidity until there is considerable lignified tissue present. For correlation with table IV we choose the rigidity curve of *D*–I, fig. 6, because the final diameter in this

TABLE IV

LIGNIFICATION TESTS; BLACK BINDWEED

No.	Internode	Length in cm. = L	Period in sec. = T	Diam. in mm. = D	$\frac{L}{T^4}$	Amount of tissue stained with phloroglucin and HCl	Corresponding points on rigidity curve; fig. 6, *D*–I
1..	n*	1.1	7.47	0.70	0.02	Only a few small vessels	.....
2..	n−1	1.7	5.03	0.85	0.07	Same as 1, only vessels larger	.....
3..	n−2, upper half	2.0	4.39	0.90	0.10	Vessels still larger and better stained	*a*
4..	n−2, lower half	2.0	1.85	1.00	0.59	Vessels about as in 3; ring of well-stained sclerenchyma	*b*
5..	n−3, upper half	1.7	1.12	1.05	1.35	Sclerenchyma better stained; more of xylem stained	.....
6..	n−3, lower half	1.75	1.00	1.05	1.75	Sclerenchyma still better stained; still more of xylem stained; more contrast between 6 and 4 than between 5 and 4	*c*

* The terminal part; the number of this internode was not determined and so is called *n*.

case is nearly the same as that in table IV. The points *a*, *b*, and *c* again demonstrate that increase in rigidity corresponds with development of lignified tissue.

Antidromous torsion

In the studies on antidromous torsion, a glass rod lubricated with vaseline was attached vertically to the apparatus, so that the frame was allowed to move upward freely but was prevented by this rod from rotating. At the same time the behavior of the midpoint of the part of the vine used was studied by means of the mirror clamp. It was found that this midpoint turned in the same direction as the frame would have done if it had been free to do so. In the case of the bean, for example, under favorable growing conditions the midpoint of an internode was found to twist through

somewhat over 360°. In the meantime a reverse twist was produced in the upper part, which continued to grow in length after the lower part had stopped. In other words, *homodromous torsion* in the lower part overpowered the younger and less rigid upper part and produced *antidromous torsion* in it.

If the frame was released before the internode had stopped growing in length, the upper part recovered to a certain extent from its reverse twist. If this was not done until full growth was attained, it recovered but little or not at all. It does not seem worth while to give results in more detail at present, but it is planned to pursue these points further by modifications of the method.

A few experiments have been made with the first internode of the flowering bean when fastened in this apparatus. It is found to twist in the same direction as other internodes, but only to a limited extent (about 90° or less). Determinations of rigidity gave the same general results as for other internodes. Hop vines were studied to some extent. The indications are that the same general conclusions hold here also, but the experiments were not very complete.

Discussion

The question of reliability of measurements and of results is first to be considered. The errors in measuring increases in length are generally negligible compared with those in other measurements. The first length, however, can be measured only to within about one mm., and this error affects all other lengths, but to a much less extent. Only the first values of rigidity and its coefficient are very much affected by it. As already mentioned, when using the mirror clamp, corresponding lengths can be measured with only fair accuracy. A careful consideration of our readings of the twist shows that these are generally accurate to within 2 or 3°. Disturbing influences, such as air currents and imperfections in apparatus, give at times greater errors than these, and account, in part at least, for slight irregularities in the curves. Determinations of the period of oscillation are generally accurate to about 1 or 2 per cent. Since the square of this value is used in the calculations, this introduces an error of about 2–4 per cent in the values for rigidity. In the last part of each experiment care must be taken to have the

part of the vine within the frame and above the upper clamp as nearly vertical as possible in order to avoid changes in the moment of inertia of the frame, and consequent error in the period of oscillation. Determinations of diameter are least accurate, only to about 3 or 4 per cent, and as the fourth power is used in these calculations, this introduces a further error of about 12–16 per cent in the values for coefficient of rigidity. Moreover, the vines are not perfectly circular in cross-section and are not of uniform texture, as would be the case with a metal wire. For this reason there are objections to the use of the terms rigidity and coefficient of rigidity, in that they do not have as definite values as in physics. When, however, these limitations are borne in mind, and it is remembered that they express relative average values only, it is believed that there should be no confusion. I believe that these errors do not vitiate the conclusions which I have drawn from the curves. It may be well to mention that similar rigidity curves were obtained when the former method of balancing twist in the vine against twist in a fine wire was used.

It may be objected that the material was studied under unnatural conditions, and that stretching introduces an unknown quantity. This is to a great extent true, but it is also true that many other investigations are made under unnatural conditions; for example, histological studies are usually made upon material that has been killed and stained. As a matter of fact, twining plants, when they can get necessary support otherwise, are sometimes observed to twist freely without much coiling or actual twining. This was observed, for example, several times in the greenhouse when a flowering bean grew near a tomato plant and found support among its leaves and branches. It must also be remembered that in ordinary twining the stem is probably subject to more or less tension. What effect, if any, is produced by the amount of tension used, and what effect, if any, the pressure of the clamps has upon the vine can be determined only by further studies.

The first part of the twist curve, which shows only a little slope, may be taken to correspond with that phase of growth which has to do largely with circumnutation, and in which there is but little twist. Torsion of the stem (but not twining proper) is generally

regarded as due to internal forces. It is evident that these forces must reside in the primary tissues, while the final stability of the internode is due to the development of secondary, lignified tissues, corresponding with the last part of the rigidity curve. Apparently lignification stops these internal forces and "sets" the stem with whatever torsion it has acquired. It is very likely that if non-twining stems were studied in a similar way with reference to rigidity similar results would be obtained.

I have not gone into morphological details because I believe that the histology of twining plants with special reference to the points mentioned deserves a more careful study than it has been possible to give it thus far. Further experiments are necessary before any more general conclusions can be drawn.

Summary

The scarlet runner bean and the black bindweed have been studied with respect to torsion in a modified form of auxanometer. It is demonstrated that, as the internode grows in length, at first it twists but little, later it twists much more rapidly, and at the end of its growth in length there is a slight reverse twist. Rigidity, or "resistance to twisting," increases only slowly until near the end of growth in length, when there is a sudden and extensive increase. This final increase in rigidity accompanies the development of secondary, lignified tissues. If we prevent the frame holding the upper part of the internode from rotating, the lower part executes homodromous torsion, and by overpowering the upper part produces antidromous torsion in it. The first internode of the bean twists only a little when held in the apparatus. In a limited portion of the vine when free to twist, the amount of torsion per unit length is about constant, but this is not true of the vine as a whole.

TRAVERSE CITY, MICH.

EARLY DEVELOPMENT OF FLORAL ORGANS AND EMBRYONIC STRUCTURES OF SCROPHULARIA MARYLANDICA

F. M. SCHERTZ

(WITH PLATES XXVII–XXIX)

The material used in this study was collected at Evanston, Illinois, in the summers of 1909 and 1915, and Bloomington, Indiana, in the summer of 1910. It was killed in medium chromic acetic acid and preserved in 70 per cent alcohol. The paraffin method was used, and difficulty was encountered because of the hardened walls of the seed case. Consequently, the walls of the seed case were dissected away, leaving the ovules attached to the axile placentae, and the difficulty was greatly lessened, although not entirely obviated because of the thick and hardened testa which remained.

Development of floral organs

The order of floral development in *Scrophularia marylandica* L. was found to be calyx, stamens, corolla, and pistil. It seems to be assumed that in the majority of cyclic flowers the parts appear in acropetal succession, namely, sepals, petals, stamens, and carpels. In *Astilbe* WEBB has observed that the order of succession of the floral parts is sepals, inner stamens, carpels, outer stamens, and petals. The origin of the petals and the stamens in *S. marylandica* is very similar to that of the flowers of the Primulaceae, in that the primordia of the petals appear after those of the stamens, and each petal apparently comes from the dorsal surface of a young stamen.

Megasporangium

The anatropous ovules arise from central placentae and develop a single integument (fig. 10). Only one layer of cells of the nucellus incloses the mother cell at this stage (fig. 11), but a marked change soon occurs, due to the growth of the integument. This

tegumentary tissue fully surrounds the megaspore mother cell, even as early as the time of the reduction division (fig. 12) of the mother cell. The greatly elongated mother cell forms the four potential megaspores (fig. 13), of which the three potential micropylar megaspores soon degenerate, while the fourth or functioning one forms the embryo sac.

The nuclei of the three degenerating cells (fig. 14) soon disappear, while that of the functional megaspore is clearly visible. In degenerating, the potential megaspore cell next to the functional megaspore disappears first; for a time it forms a sort of cap upon the functional megaspore cell. The three degenerating cells stain very heavily, while the megaspore cell stains lightly. These degenerating cells, which stain deeply with safranin, are last observed as a strip of red above the functional megaspore.

Nucellus

While the megaspore mother cell is being formed (fig. 11), a layer of nucellar tissue envelops it. The rapidly developing integument soon surrounds the nucellus and its mother cell. The cells of the nucellus are long and narrow, and their transverse walls are usually oblique.

A similar tissue arises in many of the other species of the Scrophulariaceae. BALICKA-IWANOWSKI (1) calls it "nucelle," and figures such a tissue in *Uroskineria spectabilis*, *Bartsia alpina*, *Pedicularis palustris*, *Klugia notoniana*, *Campanula rotundifolia*, and *Marina longifolia*.

The contents of these cells stain with Delafield's haematoxylin less heavily than the four megaspore cells, and less than the cells immediately surrounding them. As the embryo sac forms, it pushes its way through the micropylar end of the nucellus layer, and when the embryo sac is fully formed the nucellus is found surrounding only the chalazal end of the sac. The nucellus disappears while the endosperm is being formed within the embryo sac. It is still apparent when the first division of the endosperm nucleus takes place, and also until after four cells of the endosperm have been formed. Cells of the nucellus were not observed to be present in later developments of the endosperm (fig. 25).

Tapetal layer

The tapetal layer appears first as a ring or band of cells surrounding the nucellus (fig. 12). The cells of the tapetal layer divide only anticlinally, and later come to form a layer of cells completely surrounding the embryo sac. The cells of this layer lie with their longer axes perpendicular to the embryo sac, while the cells of the nucellus layer within them lie with their longer axes parallel with the embryo sac. This layer of cells is more persistent than the nucellus, and is observed even after most of the endosperm is formed. When the embryo approaches maturity no traces remain of the tapetal layer. These cells possess large nuclei and are well filled with protoplasmic contents. In all of the species of this group as figured by BALICKA-IWANOWSKI, this tapetal layer is shown. The extent to which the tapetal layer incloses the embryo sac varies. In *S. marylandica* the tapetum almost surrounds the embryo sac, or at least to a greater extent than it does in any of the species as figured by BALICKA-IWANOWSKI.

Nutritive tissue

In some species, as *Scrophularia vernalis* and *Scoparia dulcis*, the micropylar end of the tapetal layer is composed of many cells and is called nutritive tissue. In *Digitalis purpurea*, *Linaria Cymbalaria*, and *Torenia Deli* no such tissue is found. At the chalazal end, where the tapetum leaves off, the nutritive tissue completely encircles the lower extremity of the embryo sac in *Scrophularia marylandica* (fig. 22) and in *Linaria Cymbalaria*. In *Scoparia dulcis* no chalazal or micropylar nutritive tissue is observed, and in *Torenia Deli* this tissue is very scanty. The cell walls of the nutritive tissue stain deeply with Delafield's haematoxylin, and the nuclei are less prominent than they are in the surrounding tissues. This seems to indicate that these cells are chemically different from the surrounding tissues.

Embryo sac

The embryo sac develops from the functioning megaspore, and comes to occupy the space formerly occupied by the three potential megaspores. The "nucelle" layer of BALICKA-IWANOWSKI,

judging from the number of cells, does not appear to divide and form new cells after the first division of the megaspore mother cell, but rather, the megaspore by dividing first into two cells (fig. 15), and then into four cells (fig. 16), develops in such a manner as to protrude from the region of the "nucelle." The embryo sac is long and narrow in its chalazal part, and is enlarged in the micropylar end. After the embryo sac reaches the 4-cell stage, as in fig. 16, the nuclei migrate, and the two micropylar nuclei go to the micropylar end of the sac and arrange themselves one on each side of the sac. The nucleus closest to the micropylar end of the embryo sac now divides to form two nuclei, from which the cells of the pear-shaped synergids arise. The other micropylar nucleus divides to form the egg nucleus and the micropylar polar nucleus. The nucleus of the egg had about the same diameter as the synergid nuclei when observed, while the polar nucleus had about twice the diameter of any of the other three micropylar nuclei.

The other two of the four nuclei migrate to the chalazal end of the sac. One of the two chalazal nuclei is found almost at the very tip end of the embryo sac, while the other is located just above it.

It is here that both of these nuclei divide to form the four antipodal nuclei. When the two nuclei divide, their spindles form with the poles toward the ends of the embryo sac rather than crosswise. The three lower nuclei (fig. 18) later become the three degenerating antipodal cells. They degenerate rapidly while the upper nucleus migrates toward the center of the embryo sac, and as it migrates, it greatly enlarges and comes to be as large as the polar nucleus from the micropylar end of the sac. The micropylar polar nucleus and the chalazal polar nucleus now fuse. In the stage before fusion, the nucleoli of both are very prominent (fig. 21), and the nucleus of each is somewhat more than two diameters of the nuclei in the synergids. The large secondary endosperm nucleus now migrates upward toward the central part of the embryo sac, where it is found later, gorged with food.

In *Digitalis purpurea* BALICKA-IWANOWSKI observed remnants of the antipodals, while in *Linaria Cymbalaria* the antipodals are distinct and persist until the complete formation of the chalazal

haustoria. WESTERMEYER, as reported by BALICKA-IWANOWSKI, says that the antipodals of the Scrophulariaceae are particularly difficult to verify.

Embryo

After fertilization the fertilized egg recedes somewhat from the micropylar end of the embryo sac. The first division takes place transversely. It is followed by a longitudinal division in the chalazal cell only. The micropylar cell next divides transversely, giving rise to the first suspensor cells. The two cells of the embryo now divide to form the quadrant stage (fig. 28). The two suspensor cells divide (fig. 34) to form a linear row of four cells, which was the largest number observed. The embryo continues to develop in the normal way to form the mature dicotyledonous type (fig. 35). At no time in its development was the embryo observed to be attached to the micropylar end of the embryo sac by an enlarged basal cell, common in dicotyledons. The embryo of *Plantago maritima* is very similar to the one just described.

Haustoria

In the lower central part of the embryo sac, the secondary endosperm nucleus divides to form endosperm. When the endosperm nucleus has divided to form four cells (fig. 24), the two chalazal cells assume the character of haustoria. The nuclei in them at first (figs. 24, 25) are very prominent, but later seem to degenerate (fig. 29), and when the embryo is fully formed the haustoria themselves entirely disappear.

When the two remaining endosperm cells divide further, they produce four prolongations, which are the micropylar haustoria. These four haustoria are cut off when the endosperm has four cells in cross-section (fig. 25). They may be regarded as absorbing and conducting organs for the transport of food to the rapidly developing endosperm from the surrounding tissues. They are gorged with food matter and react strongly to Delafield's haematoxylin stain. Thickenings of the protoplasm occur in the older haustoria, and may be considered as degenerating nuclei. The nutritive cells of the ovule at the chalazal end of the embryo sac, it may be inferred, are disintegrated by enzymes secreted by the haustoria. Of the

micropylar and the chalazal haustoria, the latter are the larger. As there are no nutritive tissues at the micropylar end of the sac, this accounts for the micropylar haustoria being less developed than those of the chalazal end of the embryo sac. The chalazal haustoria also have a greater region of nutritive tissue from which to absorb. The haustoria attain their greatest development when the endosperm is being formed most rapidly. As the embryo reaches maturity only traces of the haustoria remain.

In the Rhinantheae and other members of the Scrophulariaceae micropylar and chalazal haustoria appear to be quite constant characteristics. The form of the haustoria and the extent to which they are developed vary considerably among the different species, for in *Melampyrum memorosum* they are very arborescent, while in some of the other species only rudimentary haustoria appear. In *Scoparia* no haustoria are noticeable. BALICKA-IWANOWSKI is inclined to think that the micropylar haustoria are not transformed synergids, while SCHLOTTERBECK, to whom reference is made, takes the opposite view. The writer interprets the micropylar and the chalazal haustoria as transformed endosperm cells.

Endosperm

The secondary endosperm nucleus migrates to the lower central part of the embryo sac, and endosperm formation begins with the division of the endosperm nucleus. The secondary endosperm nucleus divides transversely to form the nuclei, and almost immediately a cell wall is formed between them. Each of the two endosperm cells now formed divides longitudinally, and thus four cells are formed. At this stage (fig. 24) the egg and the two synergids were still observed at the micropylar end. The lower two of the above four cells form the haustoria, while the upper two divide transversely and then longitudinally to form eight endosperm cells (fig. 25). At this stage four haustoria are observed at the micropylar end of the embryo sac. They are put out as prolongations of the four micropylar endosperm cells. One cannot regard the micropylar haustoria as transformed synergids. Rapid nuclear division now ensues without reference to these rows of endosperm cells. Endosperm formation takes place before the first division of the egg. As the embryo matures, the surrounding endosperm storage cells

greatly thicken their walls, and their contents consist now of crystalloid protein materials (fig. 36) along with other stored foods.

When the endosperm is formed, it first occupies only the space outlined by the early stage of the embryo sac (fig. 22). As the development of the endosperm proceeds, enzymotic processes set in and the tapetal cells, along with several layers of cells just without, are absorbed and changed into endosperm structure. When the endosperm consists of only two layers of cells throughout the length of the embryo sac (figs. 29, 30, 32), several layers of cells are evident in the surrounding tissues. At a later stage (fig. 33) 8–10 layers of cells were observed in the cross-section of the endosperm, and then not so many layers (3–6) of cells were found in the surrounding tissues. It is evident that the endosperm tissue is being increased at the expense of the surrounding layers of cells. The egg up to this time has not divided. When the egg divides, the endosperm (fig. 26) in cross-section is many layers thick, while the remaining cells of the surrounding tissues have collapsed and become compressed into a thin layer. The cells at the end of the embryo sac are not so greatly changed as are the cells surrounding the sides, and even when the embryo is mature, the cells at the ends of the sac are still noticeable but are slightly compressed. At about the time of the quadrant stage of the embryo (fig. 28), enzymes are secreted and the endosperm tissue surrounding the embryo, extending greatly toward the chalazal end, becomes disintegrated. At this stage the embryo grows rapidly, and soon the cotyledons differentiate. The embryo is now found lying within the endosperm.

The cells of the endosperm are of two types. Those which immediately surround the embryo are long and narrow and mostly devoid of all protein matter, their relation to the embryo evidently leading to a loss of all their cell contents. The cells surrounding these have greatly thickened cell walls and are gorged with protein crystals (fig. 36) and other stored foods. The endosperm is entirely surrounded by a thick hardened coat which stains heavily with Delafield's haematoxylin, and from all appearances serves to protect the seed from loss of moisture. This coat is the testa. Remnants of the single integument persist as an outer covering composed of two or more layers of cells.

One of the rows of cells of the integument has become modified and now appears as a loosely scattered row of cells which connects the outermost layers of cells with the inner thickened hardened layer. Compressed cells, the remnants of the micropylar and the chalazal ends of the embryo sac at the time of fertilization, persist in the seed at each end just outside of the endosperm. The layers of cells covering the seed of various members of the Scrophulariaceae are described by BACHMAN. The number of layers of the testa of the seeds of the 128 species which he describes varies from one to four.

Summary

1. The order of the development of the floral parts of *Scrophularia marylandica* is calyx, stamens, corolla, and pistil. The stamens and the corolla arise from a common outgrowth.

2. The archesporium of the megaspore consists of a single hypodermal cell, which functions as a megaspore mother cell.

3. The megaspore mother cell by two successive divisions gives rise to an axial row of four potential megaspores; the embryo sac arises from the chalazal one, while the other three degenerate.

4. The mature embryo sac contains one egg, two large synergids, an endosperm nucleus, and three antipodal nuclei which soon degenerate.

5. A secondary endosperm nucleus, which grows larger as it migrates toward the egg, was observed. A polar nucleus from the chalazal end was seen to fuse with a polar nucleus from the micropylar end.

6. The first division of the fertilized egg is transverse, and is followed by a longitudinal division of the chalazal nucleus, while the other nucleus fails to divide until later.

7. The nucellus consists of a single layer of cells which surrounds the megaspore.

8. A tapetal layer develops around the embryo sac. It is one cell thick and begins to form at the time the megaspore mother cell divides. At the chalazal end an extensive nutritive layer is formed at the same time.

9. Two well developed haustoria are formed at the chalazal end of the embryo sac. Four less developed ones are formed at the micropylar end of the embryo sac.

10. Only a single thickened integument is found.

11. Endosperm formation takes place before the fertilized egg divides. Endosperm cells separate the fertilized egg from the micropylar end of the embryo sac.

12. The embryo develops a short suspensor which disappears as the embryo matures.

13. The mature seed consists of an embryo surrounded by thickened endosperm cells greatly gorged with crystalline protein and other food matter.

The writer is indebted to Professor C. B. ATWELL, of Northwestern University, under whom this work was conducted, for the material upon which the work was done, and for his helpful suggestions and kind advice.

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EXPLANATION OF PLATES XXVII–XXIX

Abbreviations used are as follows: *a*, antipodals; *b*, bract; *c*, cotyledon; *co*, corolla; *d*, degenerate nucleus; *e*, embryo; *f*, funiculus; *h*, haustoria; *i*, integument; *j*, endosperm; *k*, micropyle; *l*, egg; *m*, megaspore; *mc*, megaspore mother cell; *n*, nucellus; *o*, ovule; *oc*, ovary cavity; *p*, pistil; *pn*, polar nucleus; *q*, placenta; *r*, rudimentary flower; *s*, stamen; *st*, stigma; *sa*, stem apex; *t*, tapetum; *u*, protein crystals; *v*, testa; *w*, synergid; *x*, calyx; *y*, suspensor; *z*, nutritive tissues.

All of the figures were outlined by means of an Abbé camera lucida on a level with the stage of the microscope. The details were drawn in freehand. The microscope used was a Bausch and Lomb with a triple nosepiece. The following combinations were used: figs. 1–10, no. 1 ocular and 16 mm. objective; figs. 11–19, 21, 27, 31, 34, and 36, no. 8 ocular and 2 mm. objective; fig. 22, no. 8 ocular and 4 mm. objective; figs. 26, 32, 33, and 35, no. 8 ocular and 16 mm. objective; figs. 23, 24, and 25, no. 8 ocular and 3 mm. objective; fig. 20, no. 12.5 ocular and 2 mm. objective. In all of the figures the micropylar end is toward the top of the plate. Figs. 22, 24, 25, and 35 are each reconstructed from several sections.

FIG. 1.—Longitudinal section of stem apex and young bract before any differentiation has taken place.

FIG. 2.—Similar section of flower with bract, showing calyx being differentiated.

FIG. 3.—Similar section of flower showing bract, calyx, and stamens.

FIG. 4.—Similar section of flower, with calyx and stamens; petals and pistil appearing.

FIGS. 5, 6.—Parts in fig. 4 at an older stage.

FIG. 7.—Ovary cavity and stigma being differentiated.

FIGS. 8, 9.—Showing common origin of stamens and petals, differentiation of ovary, and relation of floral parts.

FIG. 10.—Section showing pistil and ovules on axile placenta.

FIG. 11.—Young ovule showing archesporial mother cell and nucellus, also integument.

FIG. 12.—Young ovule showing megaspore mother cell.

FIG. 13.—Axial row of 4 megaspores; nucellus, tapetum, and integument also shown.

FIG. 14.—Axial row of 4 megaspores; 3 micropylar ones degenerating.

FIG. 15.—Two-nucleate embryo sac.

FIG. 16.—Four-nucleate embryo sac.

FIG. 17.—Micropylar end of mature embryo sac.

FIG. 18.—Chalazal end of mature embryo sac.

FIG. 19.—Embryo sac showing antipodal polar nucleus, two synergids, egg, and micropylar polar nucleus.

FIG. 20.—Two synergids and egg.

FIG. 21.—Fusion of 2 polar nuclei.

FIG. 22.—Ovule just before fertilization and its relation to nucellus, tapetum, and nutritive tissue; funiculus also indicated.

FIG. 23.—First division of endosperm nucleus forming 2 cells.

FIG. 24.—Four cells of endosperm; 2 chalazal ones later form haustoria.

FIG. 25.—Two chalazal haustoria; the 4 micropylar haustoria and the 8 endosperm cells separating the haustoria.

FIG. 26.—The 3-celled embryo in surrounding endosperm cells in longitudinal section.

FIG. 27.—The 3-celled embryo; single cell later forms suspensor, while the 2 cells later form embryo.

FIG. 28.—Cells dividing to form quadrant stage; 2 suspensor cells shown.

FIG. 29.—Relation of chalazal haustoria to nutritive tissue; tapetum and endosperm cells.

FIG. 30.—Relation of micropylar haustoria to tapetum.

FIG. 31.—Cross-section through central region of embryo sac showing endosperm division into 2 rows of cells throughout the sac.

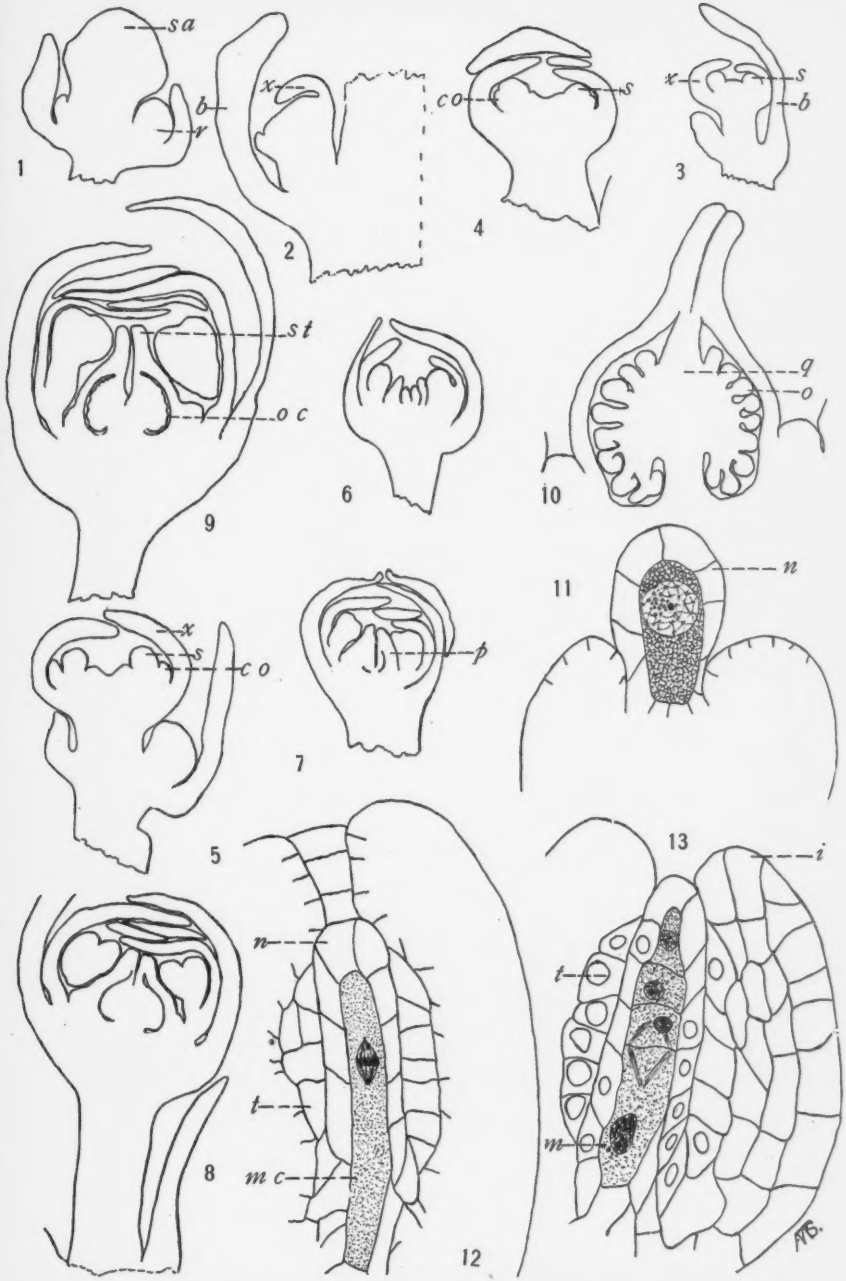
FIG. 32.—Outline drawing showing micropyle, funiculus, and relation of the 2 rows of endosperm to rest of ovule.

FIG. 33.—Later stage showing increase of endosperm in proportion to rest of ovule.

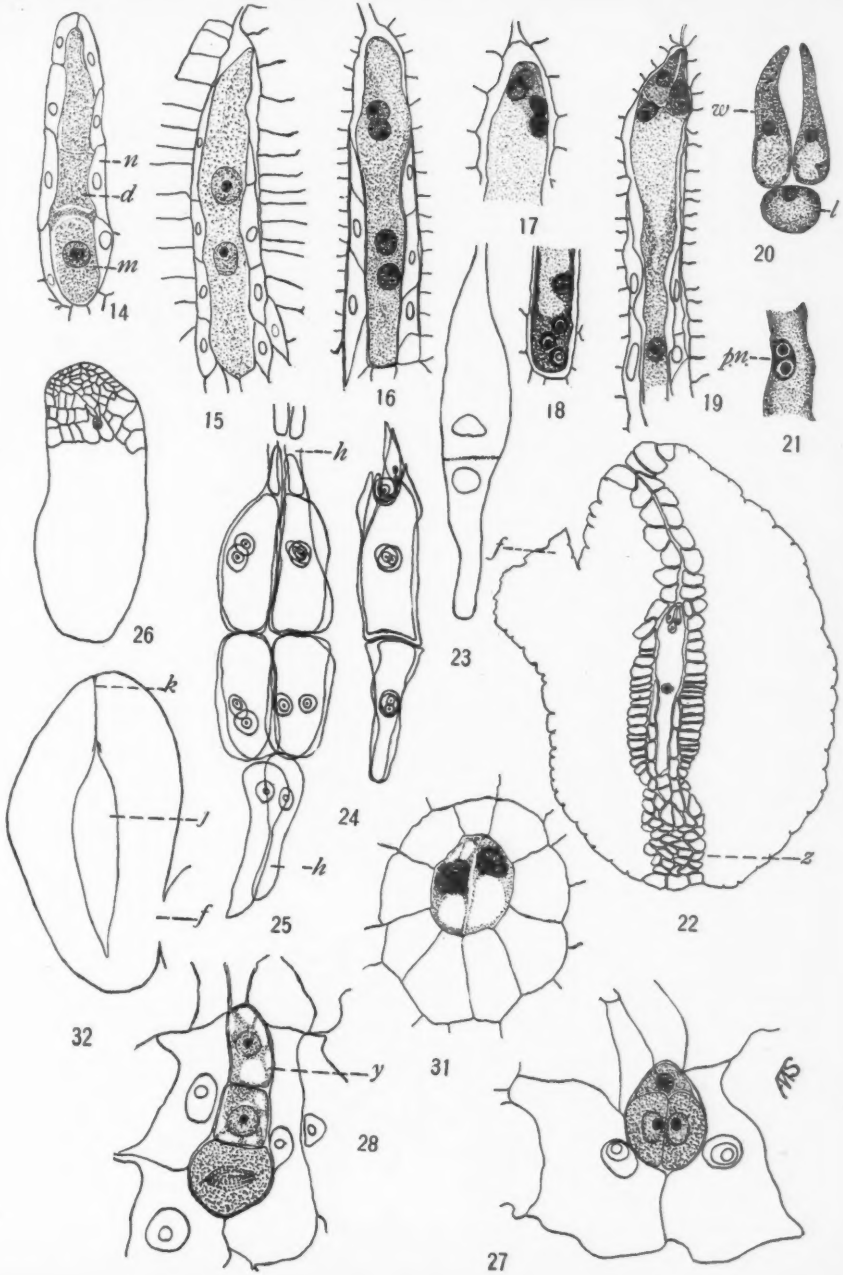
FIG. 34.—Young embryo showing the 4 cells in suspensor.

FIG. 35.—Cross-section through mature seed showing embryo, thickened endosperm cells filled with protein, and remains of integument which now functions as the testa.

FIG. 36.—Enlarged drawing of thick-walled protein-filled endosperm cells.



SCHERTZ on SCROPHULARIA



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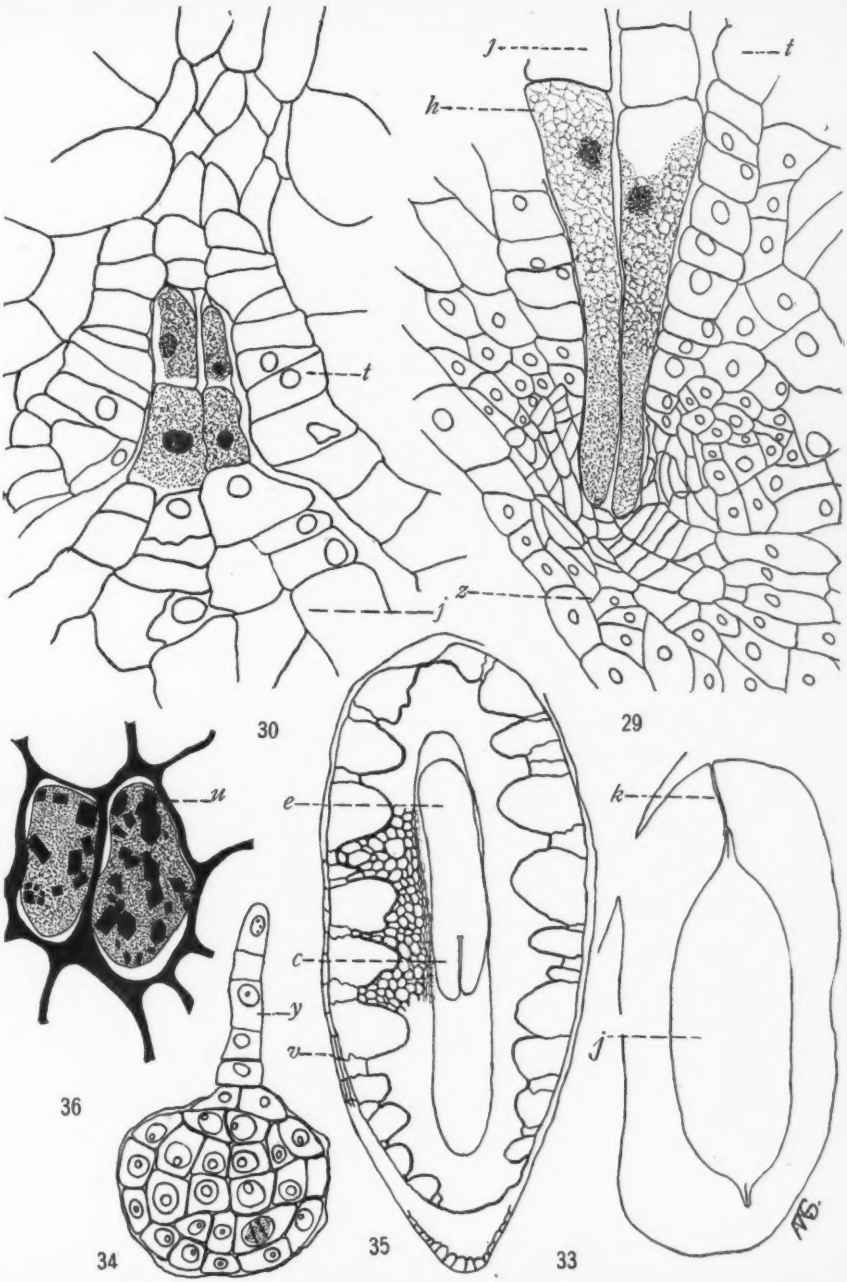

SCHERTZ on SCROPHULARIA

COMPANION CELLS IN BAST OF GNETUM AND ANGIOSPERMS

W. P. THOMPSON

(WITH SEVEN FIGURES)

The presence of companion cells in the bast of angiosperms is one of the constant anatomical features which distinguish that great group of plants from the gymnosperms. On account of the technical difficulties in the study of bast tissue in general, little emphasis has been attached to this distinction, although it is really quite as valuable as the familiar one based on the presence of vessels in angiospermic wood. The elements in question are designated companion cells, because almost invariably one of them is associated with each sieve tube. They are small, vertically elongated, parenchymatous cells which have special characteristics that will be described later, and which have no counterpart in the bast of gymnosperms.

In a study of the anatomy of the Gnetales (3, 5), it became clear that the same elements or ones remarkably similar are to be found in the bast of *Gnetum*. Another clear-cut characteristic is therefore added to the long list of features in which *Gnetum* departs from gymnospermic structure and resembles angiosperms. It has been shown (5), however, that one of the most striking of these resemblances, the possession of vessels, is not the result of a genetic connection between *Gnetum* and angiosperms, because the vessels have been evolved in entirely different ways in the two groups. It becomes necessary, therefore, to examine and compare the angiospermic and Gnetalean companion cells both as to structure and as to development.

Companion cells of angiosperms

Angiospermic bast as found in *Aristolochia macrophylla* (Lam.) is represented in fig. 1. Two chief kinds of elements are visible: the clear, irregularly shaped sieve tubes, and the richly protoplasmic parenchymatous cells (in most sections of bast there are

in addition thick-walled fibers constituting the so-called hard bast). The parenchymatous elements are in turn plainly of two kinds: large cells containing starch grains, which are represented in black as if stained with iodine, and much smaller, starchless elements. The latter are the companion cells, whereas the former are ordinary storage parenchyma. A further difference between the two kinds appears in longitudinal sections; the companion cells are highly elongated vertically, while the ordinary storage parenchyma cells are rectangular. It should be noted that a

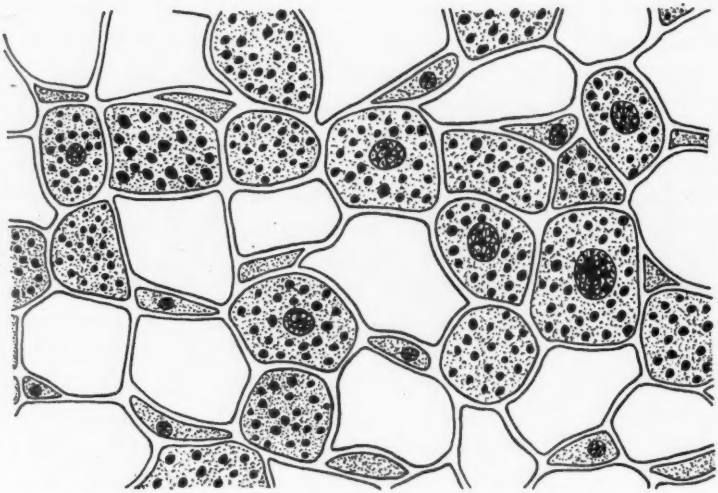

FIG. 1.—Mature bast of *Aristolochia macrophylla* (Lam.); ×1000

companion cell is associated with each sieve tube and is frequently fitted snugly into one corner of the tube.

The bast of *Aristolochia* was chosen for illustration because its elements exhibit a more orderly arrangement than is usual in angiosperms. In many species the rows of phloem cells formed at the cambium very quickly become so distorted that the orderly sequence is lost, and the cells of the mature bast then appear to be haphazardly placed. In *Aristolochia*, however, the rows of cells are to a certain extent preserved in the mature bast, as may be seen in fig. 1. When this is the case, there is a significant

indication of relationship between sieve tube and companion cell. The relative positions of these two elements is such as to indicate that they are formed from two successive cells in a row, and that they are products of the same mother cambial cell. This relationship was mentioned long ago by DEBARY (1): "Both from their arrangement in cross-section and on tracing them in the longitudinal direction, it often has the appearance as if the cambiform cells arose with the elements of the sieve tubes from one mother

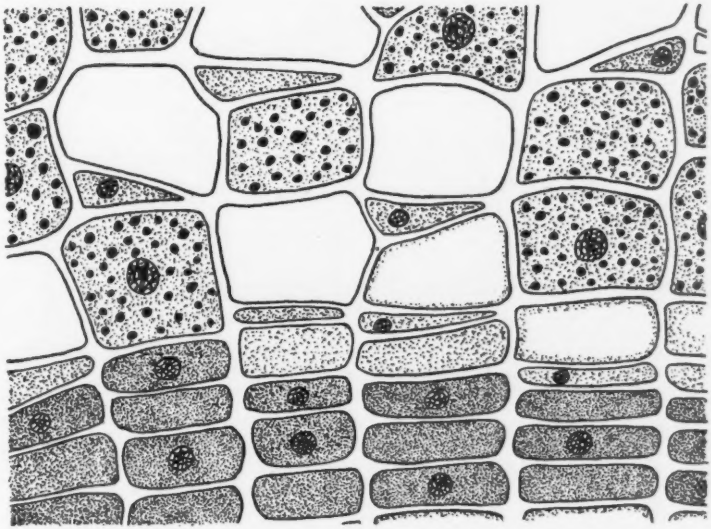

FIG. 2.—Cambium and young bast of *Aristolochia macrophylla* (Lam.) showing each sieve tube and its companion cell formed from contiguous cells in same row; ×1000.

cell, the latter dividing longitudinally into a daughter cell which becomes the sieve tube element, and another which becomes a cambiform cell without further division or is divided by cross walls into several of them." STRASBURGER (2) later made the definite statement that companion cells and sieve tubes are sister cells.

This statement is of course to be confirmed or disproved by an examination of the method in which the bast develops in the cambial region. The process as it occurs in *Aristolochia* is illustrated in fig. 2. As one traces the rows of cambial cells in the

lower part of the figure into the bast of the upper part, it becomes perfectly clear that each sieve tube and its companion cell are derived from contiguous cells in the same row, and that as the bast matures the companion cell tends to become shifted to one corner of the sieve tube. I have not been able to show that sieve tube and companion cell are products of one division. In fact, judging from what we know of cambial activity, it seems more probable that they are products of two successive divisions, in

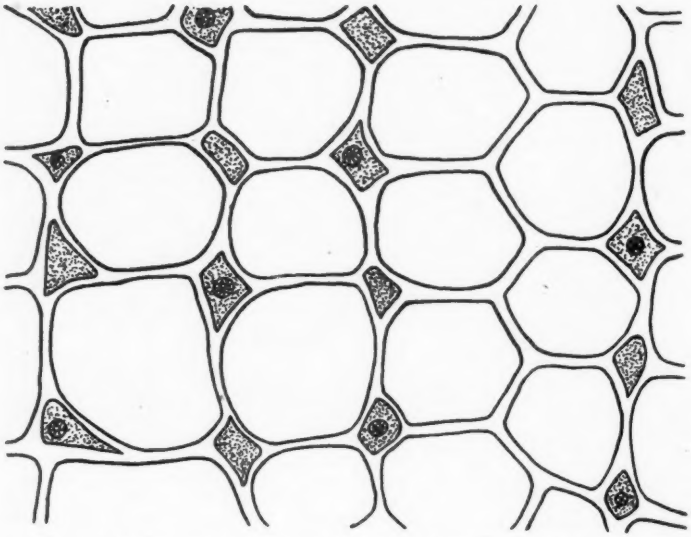

FIG. 3.—Mature bast of *Gnetum latifolium* showing sieve tubes and companion cells; ×1000.

each of which one daughter (the innermost) remains cambial. In other words, they are probably not sisters but aunt and niece. However that may be, for the purposes of the present discussion the important conclusion is that they are successive members of a single row of cambial products.

Companion cells of Gnetum

The mature bast of several species of *Gnetum* (fig. 3) consists of only two kinds of elements, large clear sieve tubes and small parenchymatous cells. The latter evidently correspond to the

companion cells of angiosperms, as is shown by their small size, their association with sieve tubes, their location in the corners of the sieve tubes, their lack of starch, and their great elongation in the vertical direction. Storage parenchyma of the ordinary type (not rays) as found in angiosperms is absent. Sieve tubes and companion cells are arranged with great regularity, the former in very uniform rows and the latter in the angles between the tubes. Usually there is an interrupted row of companion cells for every row of sieve tubes, but occasionally the former are lacking, as may be seen toward the right of fig. 3.[1]

The development of the bast at the cambial region is illustrated in fig. 4. It will be seen that the companion cells are formed in radial rows which are continuous through the cambium, and that in these rows sieve tubes are not formed. There is a tangential alternation of cambial rows which form sieve tubes with cambial rows which form companion cells. Both are never formed in the same row. As the bast matures and the sieve tubes expand, the rows of companion cells become interrupted and the individual cells pushed to the corners of the sieve tubes.

This process is evidently quite different from that which occurs in angiosperms, because in the latter sieve tube and companion cell are invariably successive cells in the same row. There is no separate cambial mother cell for the companion cells. Thus the similar mature condition is brought about in quite different ways in the two groups.

A study of the wood adjacent to the cambium, also illustrated in fig. 4, reveals an unexpected relationship between the companion cells and the parenchyma of the wood. The same cambial rows which form companion cells outwardly also form rows of wood parenchyma cells inwardly. The latter with their protoplasm are easily distinguished in the figure from the empty, thick-walled wood fibers which are formed in rows by the same cambial cells which form sieve tubes. The rows of wood parenchyma formed in this way are readily mistaken for uniseriate rays, but longitudinal

[1] It may be remarked that the bast of *Gnetum* is extremely favorable material, both for original study and for class use. The sieve areas are remarkably abundant and of great size, and the individual pores are very large and clear. Moreover, the whole tissue and the connected cambium are not easily crushed in sectioning.

sections show that they are typical, vertically elongated wood parenchyma. The rays of *Gnetum* are multiseriate or broad.

The appearance of this parenchyma in the mature wood is shown in fig. 5. At the end of the season's growth, where the fibers are small and vessels lacking, the wood parenchyma forms continuous rows (lower part of figure), but with the increase in size of the fibers and the introduction of vessels at the beginning of the next season's growth, the parenchymatous cells become

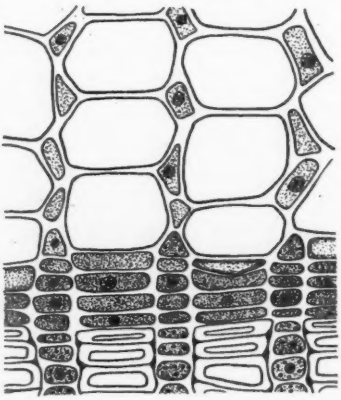

FIG. 4

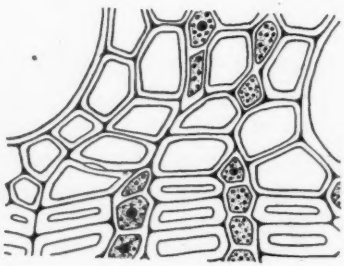

FIG. 5

FIGS. 4–5.—Fig. 4, wood, cambium, and young bast of *Gnetum latifolium* showing sieve tubes and companion cells formed from different rows of cambial cells; also wood parenchyma formed inwardly from those cambial cells which form companion cells; ×1000; fig. 5, wood of *Gnetum latifolium* showing radial rows of wood parenchyma; ×1000.

separated just as do the companion cells of the bast. Often where the vessels are large the rows of elements of all sorts become so distorted that they can no longer be traced. The elements then appear to be haphazardly arranged.

In certain regions of some species of *Gnetum* particularly interesting and primitive conditions of the companion cells are found. In the root of *G. scandens*, for example, the companion cells do not become separated and relegated to the corners of the sieve tubes, but form continuous rows, even in old bast. This condi-

tion of affairs is illustrated in fig. 6. At the top of the figure, although the bast is old and beginning to collapse, the companion cells are still in continuous rows. This condition is frequently found in roots, young stems, and reproductive axes. It evidently represents a retention of a primitive condition.

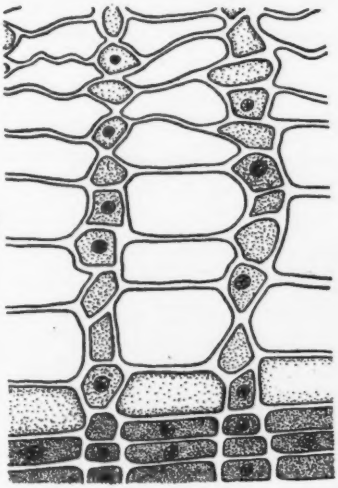

FIG. 6

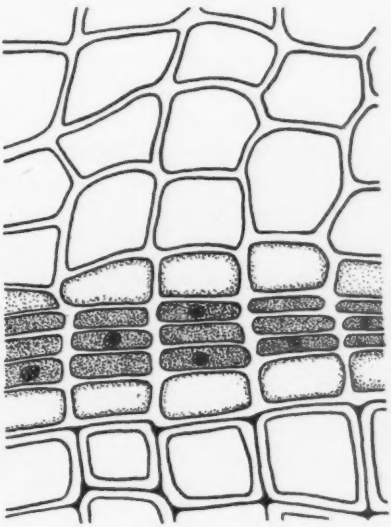

FIG. 7

FIGS. 6–7.—Fig. 6, cambium and bast of root of *Gnetum scandens* showing uninterrupted rows of companion cells; ×1000; fig. 7, wood, cambium, and bast of young stem of *Gnetum moluccense* showing absence of companion cells and wood parenchyma; ×1000.

Again, in certain regions of some species companion cells are entirely absent, the bast then consisting entirely of sieve tubes and rays. This is illustrated in fig. 7, from the young stem of *G. moluccense*. When this is the case, wood parenchyma is also lacking, as might be expected from the relationship which has been shown to exist between companion cells and wood parenchyma. The absence of companion cells has been noted in seedlings of several species and in reproductive axes, as well as in roots and young stems.

Discussion

The presence in the bast of *Gnetum* of companion cells which are in most respects of the angiospermic type is at first sight another striking indication of real relationship between *Gnetum* and angiosperms. They are to be compared with the vessels of the wood, broad rays, general habit, style (4), absence of archegonia, free-nucleate embryo sac, endosperm formation (4), and other reproductive characters. In regard to all of these points *Gnetum* is angiospermic.

The study of the development of the companion cells, however, shows that the resemblance does not necessarily indicate genetic relationship. Whereas the companion cells of angiosperms are formed from the same row of cambial cells as are the sieve tubes, and each one is contiguous to a sieve tube in such a row, those of *Gnetum* are formed in rows quite separate from the sieve tubes and are the products of different cambial cells. Of course, it is possible that the companion cells of *Gnetum* are really genetically related to those of angiosperms, and that, after originating in *Gnetum* in the method described, their formation has later been taken over in angiosperms by the same cambial cells that form sieve tubes. On the other hand, it seems more logical to conclude that we are dealing with a case of parallel evolution, just as I have shown to be true with regard to the vessels of the wood (5). The vessel of *Gnetum* with a single large perforation in the end wall is almost identical with that of many angiosperms. Nevertheless, it has been evolved in an entirely different way. The perforation of the angiospermic porous vessel has resulted from the breaking down and disappearance of scalariform bars, whereas that of *Gnetum* has resulted from the enlargement of typical, circular, haphazardly arranged, bordered pits accompanied by the disappearance of the middle lamellae, the enlargement proceeding until the intervening portions of the vessel wall have vanished. In the case of the companion cell we seem to have a close parallel to that of the vessel. While the completed structure is similar to that of angiosperms, the course of its development is quite different.

If two such striking points of resemblance as vessels in the wood and companion cells in the bast are really results of inde-

pendent evolution in *Gnetum* and angiosperms, the inference is natural that other resemblances may be in the same category.

Summary

1. Companion cells resembling those of angiosperms in size, in their association with sieve tubes, in their usual location in the angles of the sieve tubes, and in their vertical elongation, are present in the bast of some species of *Gnetum*.

2. The development of these companion cells, however, is quite different from that found in angiosperms. Whereas, in the latter, each sieve tube and its companion cell are derived from two successive cells in a single row of cambial products, in *Gnetum* sieve tubes and companion cells are produced from different rows of cambial cells.

3. Although the completed forms of companion cell in the two groups are similar, they have probably been independently evolved.

4. Primitive conditions in which companion cells are lacking, or in which continuous rows of companion cells are present, are found in certain regions of some species.

5. The parenchyma of the wood is formed by those cambial cells which form companion cells; the distribution of the wood parenchyma is consequently in radial bands, which frequently become interrupted by the expansion of vessels and fibers.

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SECRETION OF AMYLASE BY PLANT ROOTS[1]

L. KNUDSON AND R. S. SMITH

(WITH TWO FIGURES)

The fact that green plants are able to absorb certain organic substances by means of the roots, and to utilize these substances, suggests the question whether the roots of plants secrete enzymes in a manner comparable to various fungi, digesting in the culture medium, etc., the various organic substances that might be supplied. Various investigators have incidentally touched the subject, but the evidence obtained is conflicting and not at all conclusive.

LAURENT (3) reported the inversion of saccharose when this sugar was present in the culture media, and he ascribed this to the enzyme invertase secreted by the roots of corn or of peas. Starch was likewise transformed, but LAURENT ascribed this transformation to diastase secreted by the seed. MAZÈ (4) reported inversion of saccharose, but in 1911 (5) he stated that there was no enzyme secretion by the roots, and that starch was absorbed directly. WOHLLEBE (8), investigating the secretion of amylase by roots, came to the conclusion that there was a very weak secretion of amylase by the root hairs, and in some cases secretion of amylase was effected by the disconnected root-cap cells. The senior writer of this paper suggested in a previous publication (2) that invertase is secreted by the roots.

In view of the indefiniteness of information on the subject, it seemed advisable to investigate the problem. The first experiments were made on the secretion of amylase, and the results obtained constitute the basis for this paper.

Pfeffer's was the nutrient solution employed. It was made up according to the following formula: $Ca(NO_3)_2$ 4 gm., KNO_3 1 gm., K_2HPO_4 1 gm., $MgSO_4$ 1 gm., KCl 0.5 gm., $FeCl_3$ 100 mg., distilled water 6 l. Merck's soluble starch was used throughout the experiments.

[1] Contribution from the Laboratory of Plant Physiology, Cornell University.

The plants were grown under sterile conditions.[2] The seeds were sterilized by the calcium hypochlorite method (7). After the seeds were sterilized, they were planted in test-tubes on sterilized

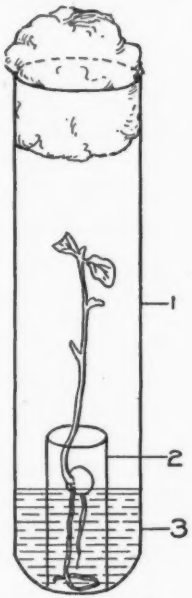

FIG. 1

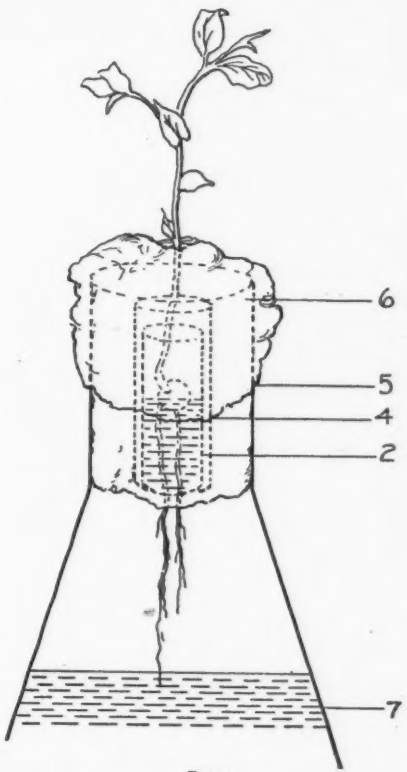

FIG. 2

FIGS. 1, 2.—*1*, sterile culture tube; *2*, germination tube; *3*, 1 per cent agar; *4*, outer tube; *5*, Erlenmeyer flask; *6*, sterile cotton; *7*, nutrient solution.

agar, as shown in fig. 1. When the seedlings were sufficiently developed, they were transferred to the culture vessels. The culture vessels used were Erlenmeyer flasks of 1 or 2 l. capacity.

[2] The writers are indebted to Dr. J. K. WILSON for the method of growing plants under sterile conditions.

The flasks were stoppered with cotton plugs, each provided with a glass tube passing through the center, this tube also being plugged with cotton. The culture flasks with solutions were sterilized in the autoclave for 30 minutes at 15 pounds pressure.

When the seedlings were of adequate size, they were transferred to the culture vessel. Transfer was made when the roots reached the bottom of the tube and were curled about, and the tops had attained a height of about 5 cm. By use of a heavy platinum needle, the tube, together with the inner core of agar and the seedling, was withdrawn from the test-tube and transferred to tube 4 of the culture vessel (fig. 2). The tube 4 was slightly drawn at the base so as to prevent tube 2 from passing through into the culture solution. Sterilized cotton was then packed about the seedling in tubes 2 and 4. The cultures when set up appeared as shown in fig. 2. After being kept for a few days in the laboratory, the cultures were transferred to the greenhouse.

The particular advantage of this form of culture, from the standpoint of studying the secretion of enzymes by the roots, is that the seeds are kept entirely out of contact with the culture solution, and any enzymes derived from the seeds are held in the agar, which with the passing of time loses its water and hardens to a flaky mass.

In spite of all the precautions taken, cultures occasionally became contaminated. All such cultures were rejected. At the conclusion of the experiment, the culture solutions were brought to the original volume and analyzed. In the first cultures, tests were made for contaminating organisms, but these and other similar experiments indicated that if the culture solutions were clear at the conclusion of the experiment there was no contamination. Consequently, in the later experiments, no platings were made of the culture solutions. Data were collected also on the weights of roots and tops. Detailed methods of procedure are described under the different experiments.

For the first experiment two cultures were set up, following the method described, using 2 l. flasks, in each of which was placed 1800 cc. of the culture solution containing 0.25 per cent of soluble starch. A variety of corn known as Leaming was employed. The

cultures were grown in a greenhouse, under favorable conditions, from November 14, 1916, to December 5, 1917. One of the cultures became contaminated, so that data were obtained from only one culture. Reducing sugar was determined by KENDALL'S method (1).

The dry weights of roots and tops were respectively 172 and 430 mg.; the total weight was 602 mg.; and the increase in weight over the original weight of the seed was 262 mg. Determinations made of the reducing sugar in 100 cc. lots of both the culture solution and the control solution gave 22.18 mg. of copper for the former, and 11.25 mg. for the latter; or an increase of 10.93 mg. of copper for a 100 cc. solution (about 6 mg. of maltose). A sample of the culture solution and one of the control, with 2 per cent of toluene added to each, were incubated for one week at 30° C., and showed no increase in reducing sugar.

In this preliminary experiment there was noted a slight increase in reducing sugar, but the increase was so small as to be without significance. Furthermore, the fact that there was no increase of reducing sugar on incubation leads to the conclusion that the enzyme amylase was not secreted into the culture solution.

The conditions of the second series of experiments were the same as for the preceding, except that liter flasks were employed as culture vessels, and 1100 cc. of the culture solution was used. A variety of white dent corn known as Boone County White was used. The cultures were grown for a period of 51 days.

At the conclusion of the experiment, the culture solutions were brought to their original volume and samples were kept for analysis. To the sample solutions was added 2 per cent of toluene, and two weeks elapsed before the solutions were analyzed for reducing sugars. Analyses were made by the Munson Walker method. Data are given in table I. The data indicate that in the culture solutions there is a slight increase in reducing sugars, but not sufficient to warrant the conclusion that there is any amylase secretion. The objection might be raised that in these cultures there can be no accumulation of reducing sugars, because they are utilized as fast as produced, which is possible; but the fact that the increase is so slight, even after two weeks of incubation, supports the theory that no amylase was present.

In the third experiment the procedure was similar to that in the preceding experiments. A white dent corn was used, and also Canada field pea. In addition to using Pfeffer's solution plus soluble starch, a number of cultures were made in which Pfeffer's solution alone was employed, to see whether any reducing sugars were secreted. Two liter flasks were used. The concentration of starch was approximately 0.35 per cent. The duration of the

TABLE I

Culture solution	Dry weight (in gm.)				Reducing sugar as CuO (in mg.)	
	Roots	Tops	Total	Gain	In 100 cc. sample	Increase per 100 cc.
Pfeffer's solution	0.6	1.05	1.65	1.3	None	None
Pfeffer's solution +0.25 per cent starch	0.5	2.1	2.6	2.3	14.5	6.4
Pfeffer's solution +0.25 per cent starch	0.5	1.7	2.2	1.9	10.0	1.9
Pfeffer's solution +0.25 per cent starch	0.7	2.15	2.85	2.55	12.9	4.8
Pfeffer's solution +0.25 per cent starch; no plant	.....	.....	.....	.....	8.1	.....

experiment was 47 days. At the conclusion of the experiment, the culture solution and the controls were made up to their original volumes, and 20 cc. portions were taken and were analyzed by Shaffer's method (**6**) for reducing sugars. Sample lots of each were also incubated with 2 per cent of toluene at 32° C. for 10 days, and the reducing sugars again determined. The data are given in table II.

There is a very slight increase in reducing sugars in some of the culture solutions over that in the control, but not enough to be of any significance. Furthermore, after 10 days' incubation there was no increase in the amount of reducing sugars.

Finally, to prove that the soluble starch is not utilized directly or indirectly to any appreciable extent, the following procedure was undertaken. Sample lots of the control and culture solutions were hydrolyzed and reducing sugars were determined. It was found that the control and culture solutions showed the same amount of

reducing sugar, which was equivalent to 73 mg. of glucose per 20 cc. of the culture solution.

In conclusion, therefore, it may be stated that neither *Zea mays* L. nor *Pisum arvense* L. is capable of utilizing soluble starch

TABLE II

Plant	Culture no.	Culture solution	Dry weight (in gm.)			Reducing sugars (in mg.)	
			Tops	Roots	Total	At termination of experiment	After 10 days' incubation
Corn	1	Pfeffer's solution alone	1.95	1.00	2.95	Trace	.....
	2		1.80	0.75	2.55	"	.....
	3		1.70	0.95	2.65	"	"
Pea	1		0.68	0.26	0.94	"	.....
	2		0.55	0.07	0.62	"	.....
	3		0.64	0.18	0.82	"	.....
Corn	1	Pfeffer's solution +0.35 per cent of soluble starch	0.7	0.4	1.10	3.4	4.0
	2		1.4	0.6	2.00	6.5	6.0
	3		1.5	0.7	2.20	3.7	4.0
	4		1.1	0.5	1.60	5.3	5.0
	5		1.4	0.6	2.00	4.4	4.0
Pea	1	Pfeffer's solution +0.35 per cent of soluble starch	0.5	0.2	0.70	3.7	4.0
	2		0.5	0.2	0.60	6.5	6.0
Control	1	No plant	.....	.....	.....	1.8	.....
	2		.....	.....	.....	3.7	.....

directly or indirectly, nor is there any appreciable secretion of amylase by the roots of these plants, at least under conditions such as were maintained for these experiments.

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RAY TRACHEID STRUCTURE IN SECOND GROWTH SEQUOIA WASHINGTONIANA

H. C. Belyea

(WITH FIVE FIGURES)

Ray tracheids are essentially a structural element in all woods of the Coniferae, and, as has been pointed out by several writers, the value of their presence or absence in taxonomy is without question. It has also been stated by several writers on this subject that as a wood structure they reach their highest development in their normal occurrence in the Pineae of the Abietineae, particularly in *Larix*, *Picea*, *Pseudotsuga*, and most notably in *Pinus*, attaining their greatest complication in the dentations and reticulations of the marginal ray tracheary cells of the hard pines. In the other two members of the Pineae, ray tracheids are normally found in *Tsuga*, but not in *Abies*. Although DeBary (1) and Penhallow (6) both described them as characteristic of *A. balsamea*, this conclusion does not seem to be borne out by the work of Thompson (7) and Miss Holden (4), who both state that ray tracheids are not to be found in this species. Thompson (7), however, reports them as occurring traumatically in *A. amabilis* and *A. concolor*.

In the Taxodineae, while they are entirely absent from *Taxodium*, they are notably present in *Sequoia*, and have been described by Gothan (3) for *S. washingtoniana*, and for *S. sempervirens* by Miss Gordon (2) and Jones (5).

In the Cupressineae they are found in all members of *Chamaecyparis*, more or less abundantly in *C. nootkatensis*, sparsely in *C. Lawsoniana*, and, according to Thompson (7), only under traumatic stimulus in *C. thyoides* and *C. plumosa*.

In the closely allied genus *Cupressus* they are much more abundant, frequently occurring as an entire ray one to three cells high. In *Thuya* they are also quite common, and in this genus are invariably marginal, with small bordered pits on their tangential walls, and slightly larger ones on their lateral end walls. In *Juniperu*

they are present very sparsely, but are readily recalled under traumatic stimulus. In this genus, according to Miss HOLDEN, ray tracheids usually occur as very irregularly walled cells, thickly pitted on the tangential walls, usually constituting a ray one cell high. According to PENHALLOW there are no ray tracheids in *Libocedrus*, but Miss HOLDEN reports them sparsely located under traumatic stimulus in wounded material from *L. decurrens*.

It is to be noted that while ray tracheid structure is an essential feature of the Coniferales, it is only constantly and normally present in the older genera. In the younger genera this structure may or may not be present, yet is invariably recalled under traumatic stimulus. This is in reality the general conclusion arrived at by THOMPSON (**8**) for *Abies*.

The foregoing résumé of the work already done in this subject is presented in an introduction to a description of a peculiar adaptation in ray tracheid structure noted in second growth wood tissue of *Sequoia washingtoniana* from the Sequoia National Forest in California. The sections were taken from the main trunk of the tree, which shows a phenomenally rapid growth not usually associated with *Sequoia*, attaining in 30 years a diameter of 19 inches at the point of section. Growth was kept up fairly regularly and consistently during the entire period.

The wood was very light in weight and very soft, was very easily cut with a knife, and capable of successful sectioning with no further treatment other than boiling. In texture the wood was harsh and coarse and somewhat inclined to be cross-grained. Sapwood was very prominent, comprising more than 90 per cent of the cross-sectional area. The growth rings were wide spaced, varying from 0.2 to 0.7 inches for a single season's growth. Microscopically the cell structure was large and thin-walled, with a very gradual transition from spring to summer wood.

As has already been stated, ray tracheid structure normally occurs in both of the present members of the genus *Sequoia*. In the mature wood of *S. washingtoniana*, two kinds of ray tracheids are to be found. First, the single, isolated, detached, radially elongated tracheary cell found on the upper and lower margins of primary rays, as is shown in fig. 1. The extent of the radial

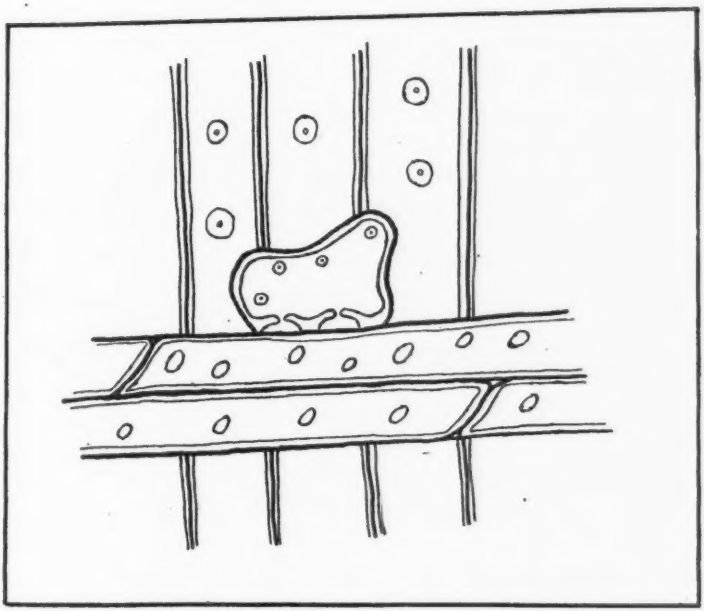

FIG. 1.—*Sequoia washingtoniana* (virgin growth): radial section showing ordinary type of isolated detached ray tracheid.

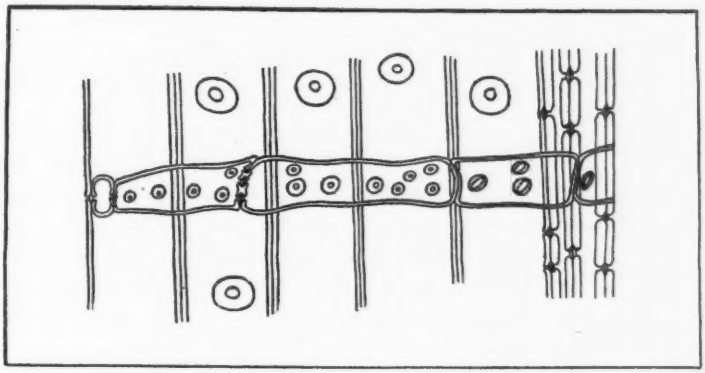

FIG. 2.—Radial section (mature wood) showing ray with two tracheid cells interspersed between ray parenchyma cells; tracheids not marginal, but components of a ray one cell high.

elongation is variable, as is also the height and the depth of the cell, which latter, however, approximates that of the ray with which it is associated. The pitting on the walls is very characteristic, especially in horizontal contact with the parenchyma cell of the ray. Second, the interspersed type of ray tracheid, as shown in fig. 2, where the tracheary cells occur in the midst of the radial prolongation of rays one cell high. They may be found singly, or in groups separated from other cells or groups of cells of similar structure by one or more parenchyma cells. Fig. 2 shows two tracheid cells occurring together with parenchymatous ray cells on either

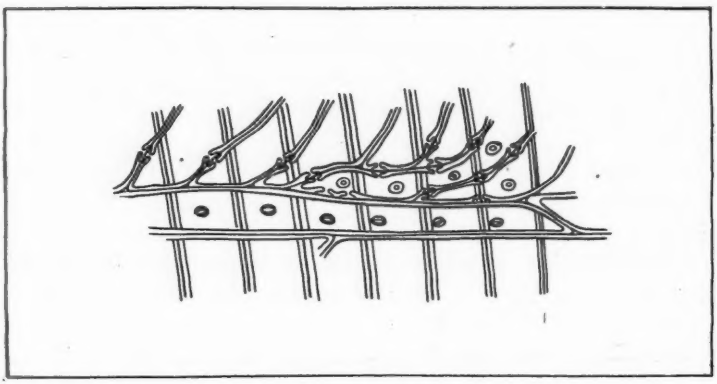

FIG. 3.—Radial section (second growth wood) showing most common form in which vertical wood tracheid is bent and prolonged along the ray to act as ray tracheid; note diversity of pitting in walls of tracheary cell.

side. In these the pitting is very characteristic, especially in the radial end walls. Miss HOLDEN has spoken of such rays as these as "secondary rays."

In contrast to the foregoing, the marginal structures on the rays of the wood of second growth *S. washingtoniana* show great variation. True ray tracheids in accordance with the previous descriptions do not occur. On the margins of the rays, however, there is a peculiar adaptation in the termination of the vertical wood tracheids directly at the ray, with the development of communicating pits in the contiguous walls of the tracheids and the

parenchyma cells of the ray. There is also evolved a radial elongation and projection of the terminating ends of the vertical tracheary elements in direction parallel to and in contact with the parenchymatous cells of the ray, with communicating pits in the intervening walls, as is shown in fig. 3. Inasmuch as true ray tracheids are not to be found, it is believed that these structures are acting as such and possess all the functions attributed to and carried on by ray tracheids.

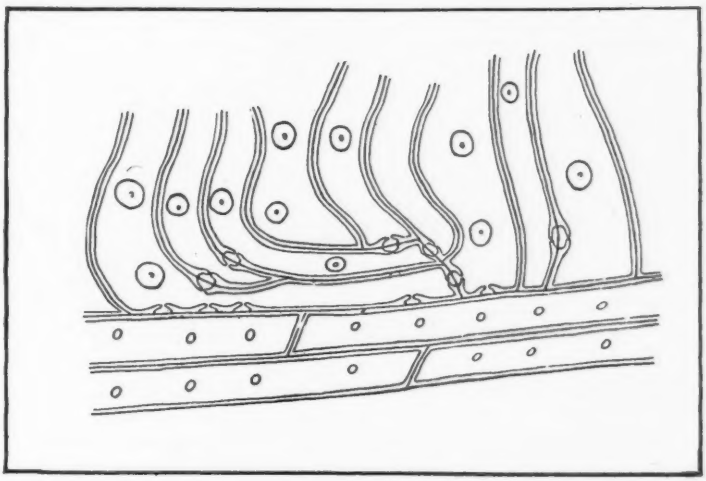

FIG. 4.—Radial section (second growth) showing wood tracheids bent and prolonged to form marginal ray tracheid two cells deep for width of two vertical wood tracheids.

It is also to be noted that in a great many cases the course of the bent-over and prolonged tracheid is imitated by those immediately contiguous with greater or less development. This is especially noticeable in fig. 4, where two neighboring and contiguous vertical tracheary elements are bent over in such a way that a ray tracheid two cells deep is evolved for the distance covered by two vertical tracheids. That these bent-over wood tracheids function as ray tracheids is evident from the double form of pitting to be found in their cell walls.

This procumbent and radial prolongation of vertical tracheary elements is to be found on either the upper or the lower margins of the rays. The direction of the prolongation may be toward the pith or toward the cambium. There seems to be absolutely no constant feature of direction which the bending shall follow, either in orientation of the one with the other or with the pith and the cambium. Along the same ray, as is seen in fig. 5, neighboring tracheids can be found bent in opposite directions and so prolonged that the end walls are in contact.

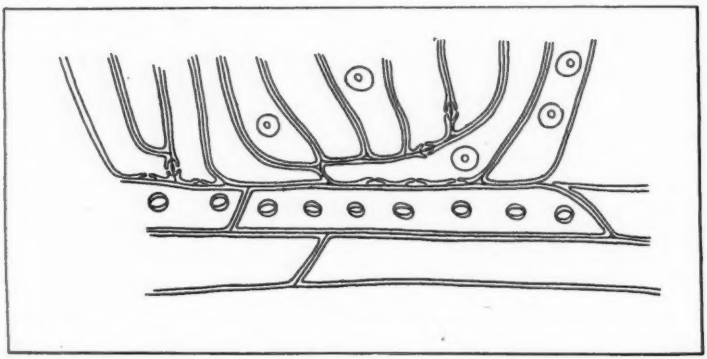

FIG. 5.—Radial section (second growth wood): adjacent wood tracheids bent in different directions along same ray.

In this second growth wood these structures were common to all parts of the stem, pith, medial sections, and cambial layers. Of the three it was perhaps least highly developed in the sections contiguous to the pith, in which there is some development of heartwood. It was found in equal frequency in either the spring or the summer wood, although, as would be expected, it was more clearly defined and capable of better figuring in the large structures of the early wood.

These structures recall and are similar to those described and figured by THOMPSON (7) in the cone axis of *Pinus Strobus*, and by JONES (5) in the mature wood of *Sequoia sempervirens*, in both of which there is ascribed similar function by the respective writers.

No attempt is made in the present article to draw any particular or general conclusions. The whole is submitted as an observation and description of a peculiar and interesting wood structure. It is to be noted, however, that these structures were found and are described in extremely rapidly grown wood tissue, and it is thought that they are special adaptations of the elements for the transference of material between the vertical and horizontal tissues, since there is an entire absence of the usual intermediary tracheary channels of communication. The origin and formation of these latter elements have been fully described and established by THOMPSON (8).

This study was undertaken at the suggestion of Professor S. J. RECORD, of the Yale School of Forestry, who also supplied a considerable portion of the material and much kindly criticism, and to whom the writer wishes to express his thanks and appreciation.

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PERITHECIA WITH AN INTERASCICULAR PSEUDOPARENCHYMA

F. L. Stevens

(WITH PLATE XXX)

Taxonomic import is attached to the presence of paraphyses between the asci in the perithecium or other ascigerous structure. For this reason, as well as on purely morphological grounds, the structure to be here described is of interest.

The collection was made March 31, 1913, at Jayuda, Porto Rico, on the common Maya (*Bromelia pinguin*). Large leaves or portions of leaves were dead and rather thickly set with intensely black bodies, which on microscopic examination were readily revealed as perithecia, bearing abundant asci. Ordinary examination of material boiled in water or in potash solution, then teased apart and crushed, showed no strikingly unusual features about the asci, except that it was difficult to decide whether or not paraphyses were really present. Material was softened in lactophenol for two days, washed, and then imbedded in paraffin through xylol, and sectioned.

From the sections it is clearly apparent that the black, thick, perithecial wall is sharply limited on its inner side, and that the central area, which in most perithecia is merely a cavity or a cavity partially filled with asci and paraphyses, is in this case occupied by a pseudoparenchyma. The perithecial wall cells are dark and thick-walled (figs. 2–3). The interascicular pseudoparenchyma is composed of thin-walled, hyaline cells, small and of quite uniform size. In relatively old perithecia with mature asci the spaces between and above the asci are completely filled with the pseudoparenchyma. In still older perithecia the interascicular pseudoparenchyma is seen to break down, beginning at the ostiole. An example of this is shown in fig. 1. As the ostiolar tissue disorganizes a mycelium penetrates down through it; whether this mycelium belongs to this fungus or to another is not known

(fig. 1). In young perithecia which do not yet show asci, the whole central portion of the perithecium is filled by the pseudoparenchyma (fig. 2). It is of interest to know how the asci develop within this structure, but the material did not afford all the evidence desired. The asci, however, are all basal and arise from any part of the base of the perithecium (figs. 3, 4), and since asci of various ages are seen imbedded in the pseudoparenchyma, it is apparent that they grow out into it; and since there is no evidence of crowding exhibited by the pseudoparenchyma cells near the asci, the asci probably digest the pseudoparenchyma as they grow forward. Indeed the pseudoparenchyma is very tenuous and is probably very easily disposed of. Fig. 4 shows an ascus that has shrunk, leaving a free space between itself and the surrounding pseudoparenchyma. The structure of this perithecium suggests the condition in the perithecium of *Penicillium* and the Plectascineae generally, where the asci are scattered in a pseudoparenchyma. This case is different, in that the asci in this fungus are not scattered but arise basally. The similarity, however, suggests a relationship between the Plectascineae and the Sphaeriales.

In the Erysiphaceae the asci develop *pari passu* with the perithecium, and at certain stages may show asci with parenchyma-like cells between them (cf. fig. 30, pl. 2., HARPER, R. A., Carnegie Inst. Publ. 37, September, 1905). In certain other fungi the young perithecium is solid throughout and pseudoparenchymatous; while later the central cells disorganize and a central cavity results. The asci push up into this cavity. Neither of these conditions presents an exact parallel with that of the fungus under consideration. A simple rational inference is to regard the case as one of delayed dissolution of the pseudoparenchymatous central region of the developing perithecium. The fact that this structure was not clearly seen without good thin sections raises the question whether similar conditions may not exist in other perithecia, and may have been overlooked because the microtome has not been employed.

The mycelium of this fungus is interesting on account of its great variation in shape and size (fig. 5). The ostiole is lined by

a fringe of projecting toothlike or clawlike cells. The perithecia often occur solitary, when they are seen to be clearly sphaeriaceous in character. Often there are two (fig. 6), more rarely three, lying together. Such considered by themselves might be regarded as dothideaceous. The fungus appears to be clearly sphaeriaceous, and owing to the peculiar character of the pseudoparenchyma I propose it as a new genus.

Desmotascus, gen. nov.—Mycelium and perithecium black, sphaeriaceous, ostiolate, short-beaked. Asci with an interascicular pseudoparenchyma, 8-spored. Spores nearly hyaline, 1-celled.

It differs from *Phomatospora* in the character of the interascicular pseudoparenchyma. Name from δεσμώτης, prisoner. The type is the following:

Desmotascus portoricensis, sp. nov.—Mycelium dark, varying in diameter from 4 to 17 μ. Perithecia 119–190 μ wide, 85 μ high, black, roughly spherical, solitary or in groups of two or three, immersed papillate or short-beaked, ostiolate. Asci 8-spored, oblong, obtuse, thickened at apex, 50–85×17 μ. No paraphyses, but the perithecial cavity filled by a pseudoparenchyma. Ascospores oblong, somewhat irregular, 20–31×8.5–10 μ, pale straw-colored.

On *Bromelia pinguin*, Mayaguez, 964 (type); 964-1 type slide.

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EXPLANATION OF PLATE XXX

FIG. 1.—Ostiole with mycelium entering and disorganizing the tissue.

FIG. 2.—Whole interior of perithecium filled with pseudoparenchyma (*h. p.*).

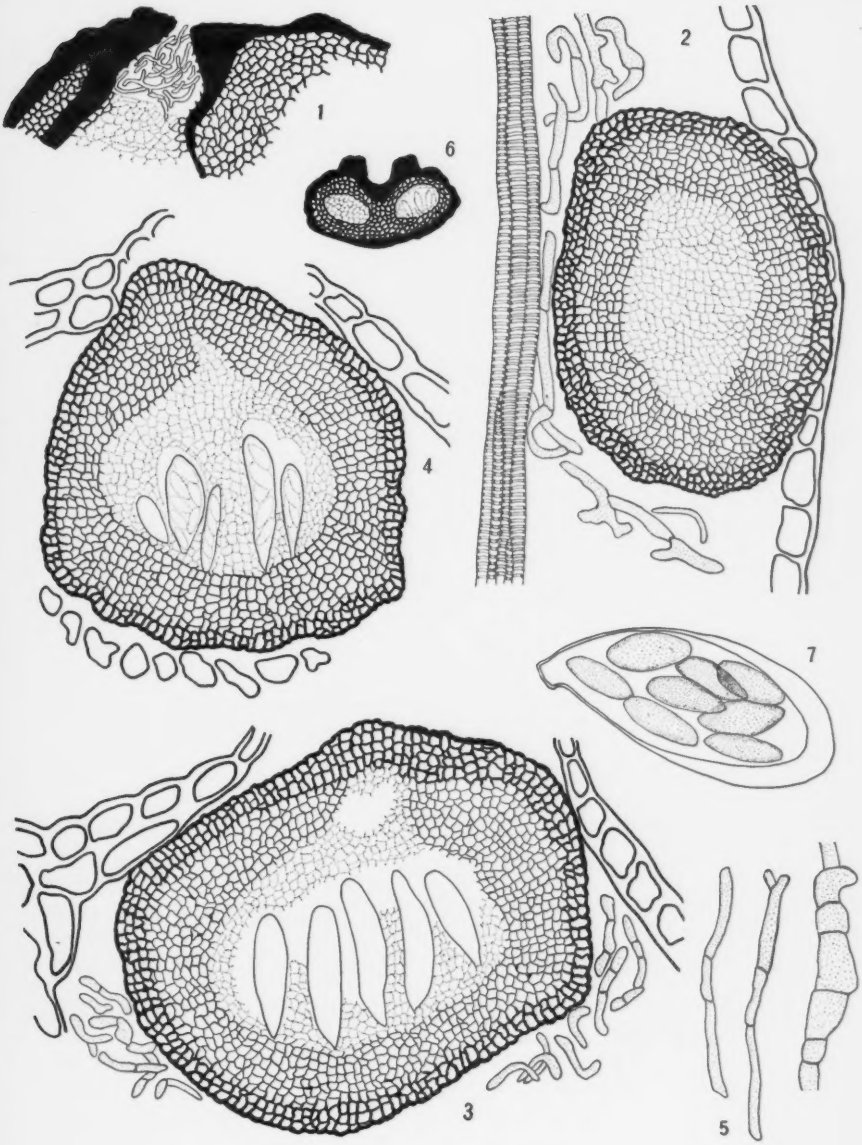
FIG. 3.—Perithecium with asci, showing origin from various parts of base of perithecium.

FIG. 4.—Showing asci shrunk away from interascicular pseudoparenchyma (*h. p.*).

FIG. 5.—Showing variation in size and shape of internal mycelium (*h. p.*).

FIG. 6.—Two perithecia showing beaks (*l. p.*).

FIG. 7.—Ascus and spores (*h. p.*).



STEVENS on PERITHECIA

CURRENT LITERATURE

BOOK REVIEWS

Plant succession

CLEMENTS has brought together in a satisfactory way and in sumptuous form the contributions of all previous workers dealing with the phenomena of succession in vegetation.[1] The work of the various students of succession is conscientiously and sympathetically presented, and with great fulness. So admirably is this work done that it will henceforth be largely unnecessary to refer to original publications, prior to the appearance of this work, in order to get the substantial views of the various authors. The work is thus a compendium of our knowledge and theories bearing on the phenomena of succession. In the field covered by this work, CLEMENTS is himself a major contributor, and in no previous work has he contributed so much new material on the subject as this work includes. No more can be attempted here than to touch a few of the high spots.

As previously, CLEMENTS treats the formation as an organism, with structures and functions like an individual plant. As compared with previous studies by the same author, greater stress is placed on development and less on habitat. To the reviewer this seems a distinct step forward, although many workers, especially in Europe, will continue to emphasize habitat as the controlling factor in classification. The formation is defined as "the climax community of a natural area in which the essential climatic relations are similar or identical." Thus CLEMENTS' formation, as here presented, departs materially from the concept of the Brussels Congress, but agrees essentially with the "climax formation" of the reviewer, and with the still earlier "climatic formation" of SCHIMPER. SCHIMPER, however, probably failed to recognize that his "climatic formation" was really the topmost member of a series of his "edaphic formations." A number of new terms of classical origin are introduced in this volume, as is the wont of the author. Perhaps the most important of these is "sere," a term used to include the entire successional series leading up to the climax. This term is used, rather than its essential equivalent "series," because of its adaptability in combination, as in xerosere (a xerarch series), etc. CLEMENTS' treatment of the term "climax" is in general harmony with the often expressed interpretation of the reviewer; "the climatic formation is the real climax of the successional

[1] CLEMENTS, F. E., Plant succession; an analysis of the development of vegetation. pp. xiii+512. *pls. 436. figs. 51.* Carnegie Institution. Washington. 1916.

development." An apparent climax, short of the true regional climax, is termed a subclimax.

The chapter in which the views of the author and the reviewer clash most sharply is the one on direction of development. CLEMENTS states positively that "succession is inherently and inevitably progressive." The reviewer is as positive in his opinion as ever that succession may be retrogressive as well as progressive, although of course progression is much more abundant and important. What the reviewer would term retrogression is for the most part by CLEMENTS termed denudation, preparatory to the initiation of another successional series. This might pass, if all such denudations or retrogressions were sudden, resulting at once in the development of a habitat initial to a progressive series. In an area that is gradually sinking, there may be a gradual retrogression from a climax mesophytic forest to a hydrophytic association, with no denudation of any sort whatever. In a review of CLEMENTS' work by TANSLEY,[2] it is shown that it would be very difficult to apply to England the idea that succession is always progressive.

Chapters follow on the classification of "seres," the climax formations of North America, past climates and climaxes, and past succession. The chapters on past climates and vegetation will be of great value, because they bring together compactly results from widely scattered sources. The theories and the applications of the author's views to the past seem very tenuous. It is difficult enough to apply ecological principles to the vegetation of the present, and it is very much too soon to work out the characteristics and successions of past floras in any but the most superficial manner.

The work is a notable one, and must be on the working table of every ecologist and plant geographer. It is unfortunate, however, that the author has allowed his splendid classical training and love for Greek and Latin to carry him so far afield. The tendency nowadays is toward increasing emphasis on the vernacular, and it is to be feared that many of the author's best thoughts and most inspiring ideas will remain hidden among words.—HENRY C. COWLES.

Botany of the living plant

BOWER[3] has put into book form his course of lectures on elementary botany given at the University of Glasgow for more than 30 years. He gives a vivid picture of the plant as a living, growing, self-nourishing, self-adapting creature.

Of the 32 chapters, 18 are devoted exclusively to angiosperms, whose complete life activity is exhaustively treated from seed "germination" to seed dispersal. In the one chapter devoted to gymnosperms only the Scots pine is treated. This seems to the reviewer to be very inadequate treatment

[2] TANSLEY, A. G., The development of vegetation. Jour. Ecol. 4:198–204. 1916.

[3] BOWER, F. O., Botany of the living plant. 8vo, pp. x+580. *figs.* 447. Macmillan Co. 1919.

of such a fundamental group. In the two chapters assigned to Pteridophytes, only the Lycopodiales and Filicales are discussed. In the two chapters dealing with Bryophytes, students of this group will be surprised to learn that in Hepaticae the sporophyte, "except in the peculiar group Anthoceroteae, does not carry on photosynthesis." A statement concerning the ventilated structures of the gametophyte of Bryophytes is likely to mislead any but intimate students of the group: "In the sporophyte of vascular plants the typical photosynthetic organ is the leaf blade with its ventilated mesophyll and stomatal control. In the gametophyte of mosses and liverworts a similarly ventilated structure is seen in the leaves of the larger mosses and in the thallus-structure of the Marchantiales. These are, however, parts of the gametophyte, and the ventilated structure is here produced mainly by involution of the outer surface, while in vascular plants it arises from intercellular splitting of the cell walls. The physiological end is the same, in both cases, but the place and means are different. Plainly these are the results of parallel evolution, or homoplasy." Had the actual facts in Marchantiales been stated, the proof of homoplasy would have been absolute. Thallophytes are dealt with in 8 chapters. In the introductory chapter a statement widely applicable to all plant phyla is made: "It must not be assumed that all the organisms grouped under a common designation are necessarily akin to one another. . . . . Lines of descent are *divergent*, and the thallophytes would appear to represent a brush of phyletic lines radiating outwards from some simpler source." The chapter on sex and heredity is presented so clearly, so free from all verbiage, that beginners can easily grasp this subject, usually considered so complex. Likewise, the chapter on alternation of generations, the land habit, and the rise and fall of the gametophyte, is a masterpiece of lucid expression.

This text is the work of a man notable for brilliant research and also for exceptional power as a teacher. It is an example of the results obtained by a long period of first-hand contact with material as well as the presentation of these results to many generations of students.—W. J. G. LAND.

Forest products

As the utilization of plant products is a matter of interest to all botanists, a book discussing the use of wood and forest products, other than lumber, should find a place in all botanical libraries. The present volume[4] is attractive in appearance, well illustrated, and carefully organized. Some idea of its scope may be obtained from such chapter headings as the following: Wood pulp and paper, Tanning materials, Veneers, Slack and tight cooperage, Naval stores, Wood distillation, Charcoal, Boxes, Cross ties, Poles and piling, Mine timber, Fuel, Shingles, Maple syrup and sugar, Rubber, Dye woods, Excelsior and cork. Under each topic the character and source of the raw material,

[4] BROWN, N. C., Forest products. 8vo. pp. xix+471. *figs. 120.* New York: Wiley & Sons. 1919. $3.75.

the tree species involved, the processes of manufacture, the marketing, the utilization, and values are discussed. Whenever any attempts have been made toward standard specifications and grading of the products, these are given in considerable detail. Statistics of production in the United States or of importation from other lands are arranged in convenient tables, and still more important for the scientist is the bibliography which is appended to each chapter. Costs of raw material, labor, overhead, and marketing are considered, as well as selling prices and total value of production; while a detailed index makes this mass of information available for ready reference.—GEO. D. FULLER.

Economic woods

RECORD'S[5] presentation of the subject of wood structure has already made his book, in its first edition, indispensable in all laboratories where the identification of wood is attempted, on the basis of its structure as revealed through the microscope. The volume has also proved equally useful in classes where the general principles of wood structure are being studied, hence an enlarged second edition will be welcomed by a considerable constituency.

Among the desirable features of the work are good clear illustrations (whose number might be increased to advantage), logical organization, concise statement, convenient tables for reference, and a well arranged, excellent bibliography, which in the present edition is brought down to 1918. The identification key has been revised and improved and appears adequate to the demands likely to be made upon it.

One of the features of the new edition is an appendix devoted to a general description of the woods of the United States and their classification on a structural basis. Tables giving the occurrence of such structures as pits, spiral markings, and tyloses in various genera and species afford convenient means of classification and of easy reference.—GEO. D. FULLER.

NOTES FOR STUDENTS

Influence of a crop on succeeding one.—HARTWELL and his associates[6] have done some very important work on the influence of crop plants on those which follow. Some crops are very injurious to those which follow them, while other successions reveal no injurious action. As is shown by an illustration on the front cover of Bulletin 175, buckwheat is greatly injured when it follows millet, but shows good development when it follows turnips. The method,

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[5] RECORD, S. J., Identification of the economic woods of the United States. 8vo. pp. 157. *pls. 6. figs. 15.* New York: Wiley & Sons. 1919. $1.75.

[6] HARTWELL, B. L., and DAMON, S. C., The influence of crop plants on those which follow. Bull. 175. Agric. Exp. Sta. R.I. State College. 1918.

HARTWELL, B. L., PEMBER, F. R., and MERKLE, G. E., The influence of crop plants on those which follow. Bull. 176. Agric. Exp. Sta. R.I. State College. 1919.

results, and significance of these experiments can best be presented by quotations from the summaries of the two bulletins:

"The general plan of the field experiment, which is the main subject of this bulletin, is to grow 16 different crops on that number of plats for two seasons prior to growing a different one of the crops over the entire area every third year. No farm manures are used, but fertilizer chemicals are applied on all plats alike, in amounts intended to supply an average of the nutrient needs of the different crops. Information regarding these needs is obtained by soil tests conducted in pots at the greenhouse and in sections of drainpipe sunk in the paths between the field plats.

"Onions occupied the entire area in 1910. If the preceding crops are arranged in the order of increasing yields of onions of the first class, it is seen that 13–17 bushels of onions per acre were produced following cabbages, mangel beets, rutabaga turnips, and buckwheat; 35 and 87 bushels following potatoes and rye; 131–178 bushels following corn, millet, onions, oats, and red clover; 240–314 bushels following squash, timothy, and alsike clover; and 406 and 412 bushels following mixed timothy and redtop, and redtop alone.

"In 1913, after the miscellaneous crops had been grown on their respective plats again for two years, buckwheat was planted on the entire area. Again arranging the crops in accordance with increasing yields, it follows that only 4–10 bushels of buckwheat grain were produced where millet, grasses, corn, and clovers had been growing previously; 13–15 bushels where buckwheat and oats were the preceding crops; 20–23 bushels where the preceding crops had been cabbage, beets, onions, rye, squashes, and potatoes; and 34 bushels following turnips.

"Alsike clover was chosen for the crop next grown on the entire area. The lowest total yields of clover hay for the two years 1916 and 1917 were 2.53–2.60 tons per acre, following the clovers and carrots. The highest yields were 4.16–4.33 tons, following rye and redtop, and two years' failure of squashes. Intermediate yields of 3.31–3.86 tons were secured following the remaining crop plants.

"The divergent effect of crops on those which follow seems not to be attributable, at least principally, to differences in the amount of nutrients removed by the crops grown previously; that is, the smallest yield may not occur after the crop which removed the largest amount of even the most-needed nutrient. The soil acidity was affected differently by the several crops and, generally, the best yields of the onion, a plant which is sensitive to conditions accompanying acidity, followed the crops giving rise to the least acidity. These indications assume added importance because of the observed fact that the effects of the crops on those which follow were much less divergent if the soil acidity was reduced by liming.

"Even if later work should prove that preceding crop effects are not important in connection with a neutralized soil, attention should nevertheless be given by the practical farmer to the very potent influences which have been

observed in the present work, for the reason that so many soils have a greater degree of acidity than existed in these experiments, and it is doubtful if they will ever be limed sufficiently to maintain them in a neutral condition."

This work should be of great interest to the ecologist and the physiologist, as well as to the agriculturist.—WM. CROCKER.

Upper Cretaceous floras.—The eastern gulf region in Tennessee, Alabama, and Georgia, discussed by BERRY[7] with reference to the Upper Cretaceous floras, includes that part of the Atlantic coastal plain bordering on the Gulf of Mexico and lying south and west of the southern Appalachian province and east of the Mississippi River. An excellent map in colors shows the exact geographic location of the different geological formations which contain determinable plant fossils, and it appears that the bulk of the fossil floras belong to the Tuscaloosa formation, with those of the Eutaw and Ripley floras meagerly represented.

The author gives a systematic arrangement of the plants found in the Upper Cretaceous of the Gulf region, with a historical sketch, an account of the lithologic characters of the materials associated with the fossils, and a discussion of the localities with plant remains. Photographs and diagrammatic sections help to elucidate the account arranged according to the different localities where plant fossils have been found. After a thorough analysis of the field observations made separately for the Eutaw, Ripley, and Tuscaloosa formations, the composition, origin, and evolution of these different Upper Cretaceous floras follow. The 151 described species from the Tuscaloosa formation represent 87 genera segregated into 48 families. The pteridophytes are represented meagerly, while the cycad-like plants, abundant in the Lower Cretaceous, are represented by a single species of *Podozamites* and *Cycadinocarpus*. Sixteen species of Coniferales of modern types, as *Pinus*, *Dammara*, *Sequoia*, occur with the curious extinct phylloclad type, *Andcovettia*, etc. The angiosperms constitute the bulk of the Tuscaloosa flora. The author explains the scarcity of the monocotyledons as largely due to the fact that the lack of differentiation of the leaf lamina and petiole precludes the regular shedding of their leaves, which are torn to shreds by the wind, and therefore unrecognizable. The dicotyledons of the Upper Cretaceous are of great interest as to their origin, for they appeared with great suddenness at the close of the Lower Cretaceous in America, Europe, and the Arctic region. The author believes that North America was near their center of radiation, with the facts in accord with their Arctic origin and with successive waves of migration sweeping southward.

Dealing specifically with the Tuscaloosa formation, BERRY emphasizes its delta character with its flora of a lowland coastal type, including a number of distinctly strand types, such as the species of *Murica*, the figs, and several

[7] BERRY, E. W., Upper Cretaceous floras of the eastern gulf region in Tennessee, Mississippi, Alabama, and Georgia. U.S. Geol. Survey, Professional Paper no. 112. pp. 117. *pls.* 1–33. 1919.

Lauraceae, Leguminosae, and Celastraceae. The members of the Myrtales also were probably dwellers in the dry or wet strand. Many of the plants probably demanded a heavy rainfall, with emphasis on the warm temperate rain forest types. Such areas as southern Japan or northern New Zealand offer many points of comparison with the Upper Cretaceous floras of the coastal plain. The climate then was equable within the limits embraced between warm temperate and subtropical. The floras of the Eutaw and Ripley formations are treated similarly by BERRY, who concludes the introductory portion of the monograph with a consideration of correlations and the presentation of a table of the distribution of the three floras minutely analyzed. The work ends with a detailed account of the fossil plants, with the description of several new species illustrated with 33 fine plates of geological scenery and fossil plants.—J. W. HARSHBERGER.

Wood structure and conductivity.—HOLMES[8] has made a quantitative study of the anatomy of ash wood, attention being directed chiefly to the size and proportion of the water-conducting elements in different parts of a shoot. As in the case of the hazel wood previously investigated by this author, year old ash shoots were selected, most of the specimens being typical coppice, stool shoots, long, thick, and unbranched. His results are presented in graphical form, a set of curves being constructed for each shoot.

Curve A gives the variation in area of the wood at selected levels along each shoot. Curve B, representing the absolute conductivity or total volume of transmitted water, is obtained by calculating the total number of vessels in a transverse section at the different levels and the average diameter of the cavities of these vessels. This curve shows a decline from the base to the apex of the shoot. Curve C serves as a measure of the specific (or relative) conductivity for water, or the percentage of wood area occupied by vessel cavities. In general this curve rises and then falls, the upper (younger) part of the stem being a better conductor of water per unit area than that nearer the base. An increase in the proportion of fibers in any part of the shoot, usually at the base where mechanical support is necessary, quite obviously lowers the specific conductivity in that portion of the stem.

In comparing the ash with the hazel wood, the writer finds in both a fall in absolute conductivity and a rise in specific conductivity from the base of the shoot to its apex, but the figures for specific conductivity are much higher in hazel than in ash, due to its greater number of conducting elements per unit area.

In the main, these results agree with those obtained by FARMER[9] for the two kinds of wood in question, in his extensive investigations for determining

[8] HOLMES, M. G., Observations on the anatomy of ash-wood with reference to water-conductivity. Ann. Botany **33**:255–264. *figs.* 7. 1919.

[9] FARMER, J. B., On the quantitative differences in the water-conductivity of the wood in trees and shrubs. Proc. Roy. Soc. **90**: 1918.

specific and absolute conductivity. FARMER calls attention further to the close resemblance between coppice-shoots and saplings of the ash and hazel in respect to their water-conducting systems, and to the difference existing between the coppice-shoots and the normal adult wood of these species.—LADEMA M. LANGDON.

After-ripening and germination of rice.—KONDO[10] has done some very interesting work on the germination of rice seeds. Seeds gathered in the milk stage and put into a germinator immediately show little germination, even after 30 days. Those stored in a condition permitting drying for 15 days, or those stored without drying for 30 days, after-ripen and show a considerable improvement in germination. With after-ripening germination sometimes exceeds 50 per cent. Seeds harvested in the yellow ripe stage show little germination when immediately placed in a germinator, but they improve in germination relatively rapidly with storage, whether the storage conditions permit drying or not, and after 4 months of storage give as good germination as seeds harvested fully ripe. Seeds harvested fully ripe germinate fairly well immediately, but are considerably improved by after-ripening. Seeds harvested dead ripe do not need after-ripening, but are immediately capable of prompt and good germination.

While drying hastens the after-ripening of seeds collected in the milk or yellow ripe stage, those after-ripening without drying finally give quicker and better germination than those after-ripened with drying. The presence of the hulls interferes with after-ripening. A few hours of sun-drying of the fresh seeds favors germination. Diffuse light has no effect on the germination of fully ripened seeds, but it favors the germination of those not fully after-ripened. Germination percentage and energy both rise with progress in the maturity and after-ripening of the seeds. Many grains of rice show abnormal germination. In many of the seeds collected in the milk stage only the radicle grows. In the yellow ripe, fully ripe, and dead ripe grains the abnormality is shown by the growth of the plumule only, often followed later by many secondary roots.

The matter of dormancy and after-ripening of cereal seeds is giving seed testers and other practical workers no little concern, especially in regions where ripening occurs during cool or wet weather.—WM. CROCKER.

Anthocyanin.—The distribution of anthocyanin in varieties of *Coleus hybridus* has been studied by KÜSTER,[11] who classifies the patterns in two groups: (1) sectional, mottled, and pulverulent; (2) areas with curved boundaries and circular flecks. These groups of patterns are traced to different origins. Patterns of the first group are traced to qualitatively

[10] KONDO, MONTARO, Über Nachreife und Keimung veschieden reifer Reiskorner. Ber. Ohara Inst. Landw. Forsch. 1:361–387. 1919.

[11] KÜSTER, ERNST, Die Verteilung des Anthocyans bei Coleusspielarten. Flora 110:1–33. 1917.

unequal cell divisions by which unlike daughter cells arise, one of which possesses ability to produce anthocyan, the other lacking it. In all future divisions of the anthocyanin-producing mutated cells, the daughter cells also inherit the power to produce the color. The contiguous mass of colored cells in a sectional, mottled, or pulverulent pattern is considered the product of a single mutant cell. If the mutation occurs at a very early stage in the life of the plant, sectorial coloration is likely to result. If somewhat later, after the main organs have been laid down, the mottled pattern results. When the cell mutation occurs very late, so that only a few daughter cells are formed by each mutant, the pattern is pulverulent.

Patterns of the second group, rounded areas, and flecks of anthocyanin occur more rarely than those of the first group. Comparison of these patterns with the first indicates that they do not arise by cell mutation. Using seed crystals as an illustration, he suggests the possibility that at certain points anthocyanin-producing "seed colloids" of unknown composition arise, and that around these central points aggregation continues, molecules or molecular groups coming from surrounding cells, which are thus left colorless. This hypothetical colloidal substance would have some direct or indirect relation to the production of anthocyanin, either as a source of building material, or as a catalytic agent.—CHAS. A. SHULL.

Quantitative nature of sex.—SCHAFFNER[12] has published some significant observations on sex intermediates. The white mulberry shows about 40 per cent pure staminate plants, 40 per cent carpellate, and 20 per cent intermediate in all gradations. Among the last, the most interesting example consists of a pure staminate tree with a single, almost pure carpellate branch, showing "that a sex reversal can and sometimes does take place in an old tissue whose cells are removed by thousands of vegetative divisions from the original zygote. It assures us that sex control is only a matter of finding out how to change the prevailing physiological state." The peach leaf willow showed only 9 per cent intermediates. These were primarily staminate, but had many catkins which were staminate only at the base and became carpellate at the end. "But on the transition zone, between the staminate and carpellate parts, the axis seemed to be neutral in regard to sex, and here bisporangiate flowers were frequently present." Also, in this neutral zone abnormal flowers were very frequent, structures developing which were partly staminate and partly carpellate. These observations serve to support the conclusions published by the author in 1910 to the effect that "sexuality is a condition and not a character" (factor). Observations of much the same nature have recently been published by STOUT.[13]—MERLE C. COULTER.

[12] SCHAFFNER, JOHN H., The nature of the dioecious condition in *Morus alba* and *Salix amygdaloides*. Ohio Jour. Sci. **19**:409–416. 1919.

[13] STOUT, A. B., Intersexes in *Plantago lanceolata*. BOT. GAZ. **68**:109–133. *pls. 12, 13*. 1919.

Absorption limits.—The conditions existing in roots while in equilibrium concentration (equal absorption and leaching of ions) with the surrounding solution have been studied by HARVEY and TRUE[14] in sweet corn, squash, peanut, and soy bean. The value of the equilibrium concentration was found to be specific for each plant. Thus for sweet corn it was $12-15\ N\times10^{-6}$, while for squash it was $35-40\ N\times10^{-6}$, and for the peanut $50\ N\times10^{-6}$. It was independent, however, of the kind of electrolyte used, or of the original concentration or volume used, provided the original concentration was non-toxic, and that the volume contained less salt than the plant requires for full growth, so that minimum limits for absorption would be reached. The electrolyte content of the solution after equilibrium has been reached is determined partly by volatile ions (CO_2) which are quantitatively equal for all plants grown under equal conditions if equilibrium with the atmosphere has been established; but it is mainly determined by the rate at which ion-producing compounds of the cell break down, and the rate of reabsorption of these ions. The behavior of roots at minimum concentrations seems to substantiate STILES' view that there are concentration limits below which the root cannot absorb enough salts, merely because the nutrient solution is too dilute.—C. A. SHULL.

Embryogeny in angiosperms.—SOUÈGES,[15] in continuing his studies of embryogeny in angiosperms, has emphasized his claim that the laws which govern development are the same in monocotyledons and dicotyledons. The investigations cited compare typical representatives of monocotyledons and dicotyledons (*Anthericum* and *Polygonum*). According to this investigator the only difference in the embryogeny of the two groups is that in dicotyledons the laws are applicable at the first division of the egg; while in monocotyledons these are not applicable until the second division, the apical cell of the 2-celled embryo being the equivalent of the egg-cell in dicotyledons. It is claimed that the variable behavior of the basal cell of the proembryo of monocotyledons accounts for the differences that have been observed. This thesis is illustrated in detail in the development of the different regions of the embryo.

It is becoming increasingly evident that embryogeny in angiosperms is not represented by two sharply contrasted methods, and these detailed results of SOUÈGES confirm other work dealing only with the cotyledon situation. —J. M. C.

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[14] HARVEY, R. B., and TRUE, R. H., Root absorption from solutions at minimum concentrations. Amer. Jour. Bot. 5:516–521. 1918.

[15] SOUÈGES, R., Embryogénie des Liliacées. Développement de l'embryon chez l' *Anthericum ramosum*. Compt. Rend. pp. 4. July 1918.

———, Embryogénie des Polygonacees. Développement de l'embryon chez le *Polygonum Persicaria*. Compt. Rend. pp. 3. April 1919.

Some oriental plants.—ROCK[16] has published an account of the endemic arborescent legumes of the Hawaiian Islands. The Islands are poor in arborescent legumes; in fact the whole family is sparingly represented as compared with such families as Rubiaceae, Rutaceae, and Lobeliaceae. The genera discussed, which include endemic arborescent forms, are *Acacia* (3 spp.), *Mezoneurum* (1 sp.), *Sophora* (3 spp.), and *Erythrina* (1 sp.). The paper includes numerous and remarkably fine photographs of herbarium specimens and of the plants in the field.

The same author[17] has presented the remarkable endemic genus *Kokia*, a relative of the cotton, in which he recognizes 3 species and a new variety. It is an interesting fact that the Malvaceae have contributed 2 endemic genera to the Hawaiian Islands (*Kokia* and *Hibiscadelphus*).

KOIDZUMI,[18] in continuation of his studies of the flora of Eastern Asia, has described 13 new species of *Pyrus* from Japan.—J. M. C.

Flora of District of Columbia.—HITCHCOCK and STANDLEY[19] have published a manual of the vascular flora of the District of Columbia and vicinity, to replace L. F. WARD'S "Guide to the flora of Washington and vicinity," published in 1881. A general description of this region shows the great diversity of conditions, resulting in an unusually interesting flora. The summary shows 1630 species of vascular plants, representing 646 genera. Of this number, 287 have been introduced, chiefly from Europe. The contribution is a series of analytical keys, so that when the name of a species is reached it has already been characterized. It is a good model for manuals intended only for the recognition of species.—J. M. C.

New tropical American plants.—In a third paper on tropical American plants, STANDLEY[20] has described 76 new species. A synopsis of the Central American species of *Erythrina* recognizes 16 species, 4 of which are new. The Mexican Mimosaceae are represented by 15 new species, 8 of which belong to *Acacia*. A synopsis of the species of *Leiphaimos* from Panama is given, 8 being recognized, 6 of which are new. *Hoffmannia* in Mexico and Central America is credited with 9 new species. The Rubiaceae of North America are increased by 7 new species in various genera. Miscellaneous species belonging to several families are also included.—J. M. C.

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[16] ROCK, J. F., The arborescent indigenous legumes of Hawaii. Board of Agric. and Forestry, Bull. 5. pp. 53. *pls. 18*. 1919.

[17] ROCK, J. F., The Hawaiian genus *Kokia*. *Idem*. Bull. 6. pp. 22. *pls. 7*. 1919.

[18] KOIDZUMI, GENITI, Contributiones ad floram Asiae Orientalis. Bot. Mag. Tokyo **33**:123–129. 1919.

[19] HITCHCOCK, A. S., and STANDLEY, P. C., Flora of the District of Columbia and vicinity. Contrib. U.S. Nat. Herb. **21**:1–329. *pls. 42*. 1919.

[20] STANDLEY, P. C., Studies of tropical American phanerogams. Contrib. U.S. Nat. Herb. **20**:173–220. 1919.

New African plants.—The continuous appearance of publications dealing with new plants from Africa is an impressive illustration of the fact that it is still largely an unknown continent botanically. MOORE,[21] in continuation of his "Alabastra diversa," has published 28 new species of African plants, belonging to the following families: Ericaceae (2), Asclepiadaceae (2), Scrophulariaceae (13, 7 belonging to *Buchnera*), Gesneraceae (1), Acanthaceae (1), Verbenaceae (5), Loranthaceae (1), Euphorbiaceae (2).—J. M. C.

Tropical American plants.—BLAKE[22] has revised the American species of *Homalium* (Flacourtiaceae), a genus valued for its timber trees and one that has been puzzling to taxonomists. He recognizes 19 species, 11 of which are described as new. In the second paper cited, 13 new species are described, chiefly shrubs or trees collected in Bahia, Brazil, and Colombia in connection with a general survey of the timber resources.—J. M. C.

New names.—MACBRIDE[23] has given a good illustration of the extensive changes of names necessary to conform to the international rules of botanical nomenclature. In reviewing portions of the Leguminosae, he has published 97 new combinations and 9 new names. In the second paper cited, which deals with miscellaneous families, 28 new combinations are published.—J. M. C.

New species of Vernonia.—In studying the tribe Vernonieae for presentation in *North American Flora*, GLEASON[24] has discovered 6 new species and 9 new varieties. He has also segregated *V. lepidota* Griseb. as a new genus (*Ekmania*).—J. M. C.

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[21] MOORE, SPENCER L., Alabastra diversa. XXXI. 1. Miscellanea Africana. Jour. Botany **57**: 212–219, 244–251. 1919.

[22] BLAKE, S. F., The genus *Homalium* in America. Contrib. U.S. Nat. Herb. **20**: 221–225. 1919.

———, New South American spermatophytes collected by H. M. CURRAN. *Idem*. 237–245. 1919.

[23] MACBRIDE, J. F., Notes on certain Leguminosae. Contrib. Gray Herb. N.S. no. 59. 1–27. 1919.

———, Reclassified or new spermatophytes. *Idem*. 28–39. 1919.

[24] GLEASON, H. A., Taxonomic studies in *Vernonia* and related genera. Bull. Torr. Bot. Club **46**: 235–252. 1919.

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Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italics*.

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